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Sexual segregation in desert-dwelling mountain sheep

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SEXUAL SEGREGATION IN DESERT-DWELLING MOUNTAIN SHEEP

A

THESIS

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By

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SEXUAL SEGREGATION IN DESERT-DWELLING

MOUNTAIN SHEEP

By

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ABSTRACT

Mountain sheep (Ovis canadensis nelsoni) were studied in the eastern Mojave Desert, San Bernardino Co., California to test 4 hypotheses potentially explaining sexual segregation in ungulates. Mature males and females were segregated from December to July, and aggregated from August to November. Mature males obtained higher quality diets than did females (based on fecal crude protein) and forage was more abundant on ranges used by these males. Indices of predator abundance were substantially lower on ranges used by females and young than on those used by mature males. Females occurred closer to permanent sources of water, and in steeper, more rugged, and more open habitats than did mature males. Female groups with and without lambs did not differ in their distance from water during aggregation or segregation. Female groups with lambs, however, occurred on steeper slopes and in more rugged and open habitats during segregation, when lambs were very young.

I refute the hypotheses that: 1) Males enhance their fitness by segregating from females and their own offspring; 2) Females outcompete males for available resources, and allometric differences between the sexes lead to sexual

segregation; and 3) The constraints of lactation may be important in explaining sexual segregation in this desert-adapted ungulate. In contrast, my observations strongly support the hypothesis that, because of their smaller body size and potentially greater vulnerability to predation, female ungulates use habitats with fewer predators and more opportunities to evade predation than do males, but males are able to exploit nutritionally superior areas.

Sexual segregation likely results from differing reproductive strategies of males and females among sexually dimorphic mammals. Males may enhance their fitness by exploiting habitats with superior forage, and thereby enhance body condition, while simultaneously incurring greater risks than do females. In contrast, females appear to enhance their fitness by minimizing risks to their offspring, albeit at the expense of nutrient intake.

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INTRODUCTION

Sexual Segregation in Ungulates

Morphological differences between the sexes long have been thought to be a mechanism to reduce intersexual competition (Darwin 1871). Moreover, the importance of sexual dimorphism in niche separation has been investigated for an array of organisms (Schoener 1966, Selander 1966, 1972, Storer 1966, Feduccia and Slaughter 1974, Freeman et al. 1976, Keast 1977, Hill and Ridley 1987, Klimley 1987, Smallwood 1987), including mammals (Bowers and Smith 1979, Gautier-Hion 1980, Fay 1982, Morris 1987, Bailey and Aunger 1989, Litvaitis 1990). The prevailing notion is that the resultant resource-partitioning reduces intersexual competition and, thereby, enhances reproductive success. Although scramble competition has been postulated as a cause of dietary differences between the sexes of some mammals (Illius and Gordon 1987), the evolution of sexual dimorphism (including allometric differences) is explained most convincingly as an outcome of sexual selection for most large, polygynous mammals (Alexander et al. 1979). Nonetheless, sexual dimorphism still may lead to a differential use of resources or space by the sexes (McCullough 1979).

The ability to exploit resources effectively must constrain the degree of sexual dimorphism brought about via sexual selection. Thus, an understanding of factors responsible for sexual segregation is necessary for a complete synthesis of how sexual selection operates and sets limits to sexual dimorphism in large, polygynous mammals. As Ralls (1977) noted, existing models of sexual selection and dimorphism derived largely from avian species simply are not applicable to many mammals.

Bierzychudek and Eckhart (1988) recently addressed the lingering question of the evolutionary significance of sexual segregation in plants, thereby emphasizing the importance of this subject to current ecological thought. Others concerned with this question have speculated about the causes and consequences of sexual segregation in large mammals (King and Smith 1980, Festa-Bianchet 1986, 1988a, 1988b, Beier 1987, Clutton-Brock et al. 1987, Scarbrough and Krausman 1988, Wirtz and Kaiser 1988, Miller and Litvaitis 1992); however, the question of cause and effect remains unanswered.

Because critical tests of hypotheses related to sexual segregation are few, Bierzychudek and Eckhart (1988) suggested that future studies of the spatial distribution of plants avoid inferring that sexual segregation is adaptive, or represents an evolved response to competition between the

sexes, until confirmatory evidence is obtained. For example, an early paper by Freeman et al. (1976) argued that male and female plants fared differently under xeric and mesic conditions, presumably a Darwinian adaptation. Careful scrutiny and critical tests of Freeman et al.'s (1976) hypothesis, however, resulted in rejection of their idea (Fox and Harrison 1981). I propose that the causes of sexual segregation in large mammals have not been investigated fully and, likewise, caution that hypotheses about sexual segregation in large mammals have seldom been tested adequately. Hence, the idea that sexual segregation evolved as an adaptation (Williams 1966) remains speculative.

Ungulates offer a unique opportunity to study the ecological consequences of sexual segregation because of the extreme sexual dimorphism exhibited by many of these mammals (Ralls 1977). Studies have documented that spatial separation of the sexes occurred for a variety of ungulates, including caribou and reindeer (Rangifer tarandus) (Cameron and Whitten 1979, Helle 1980, van Wieren and de Bie 1980, Skogland 1989), red deer and elk (Cervus elaphus) (Peek and Lovaas 1968, Boyd 1978, Clutton-Brock et al. 1982, Geist 1982), mule deer (Odocoileus hemionus) (Bowyer 1984, Ordway and Krausman 1986, Scarbrough and Krausman 1988), white-tailed deer (Odocoileus virginianus) (Dusek et al. 1989,

McCullough et al. 1989, LaGory et al. 1991), moose (Alces alces) (Edwards 1983, Miquelle et al. 1992), giraffe (Giraffa camelopardalis) (Pellew 1984, Du Toit 1990, Young and Isbell 1991), bison (Bison) (Guthrie 1990), Cape buffalo (Syncerus caffer) (Sinclair 1977, Prins 1989), Tibetan antelope (Panthelops hodgsoni) (Schaller and Junrang 1988), pronghorn (Antilocapra americana) (Kitchen 1974), waterbuck (Kobus ellipsiprymnus) (Wirtz and Kaiser 1988), chamois (Rupicapra rupicapra) (Shank 1985), mountain goat (Oreamnos americanus) (Holmes 1988), mouflon (Ovis ammon) (Bon and Campan 1989), and mountain sheep (Ovis canadensis) (Ober 1931, Welles and Welles 1961, Geist 1971, Geist and Petocz 1977, Morgantini and Hudson 1981, Ashcroft 1986). Only recently, however, has research been designed specifically to address the causes of sexual segregation (e.g., Shank 1982, Bowyer 1984, Beier 1987, Clutton-Brock et al. 1987, Miquelle et al. 1992). Moreover, because of allometric differences among mammals (sensu Clutton-Brock and Harvey 1983, Peters 1983), it is unlikely that the ecological determinants of spatial separation of the sexes will be the same for small and large-bodied species. Thus, hypotheses or models that explain the population characteristics of small mammals may not suffice for large ones (Caughley and Krebs 1983, Millar and Zammuto 1983).

For this research, I studied a population of desert-dwelling mountain sheep (O. c. nelsoni) to test 4 hypotheses that have been posited to explain sexual segregation among ungulates. Desert-dwelling mountain sheep are ideal for studying sexual segregation because they: 1) Exhibit extreme sexual dimorphism; 2) Do not shed their horns and, thus, are easily distinguishable as adult males or females throughout the year, even from great distances; and 3) Show pronounced and prolonged spatial separation of the sexes.

Biology of Mountain Sheep in Desert Environments

Mountain sheep generally are associated with mountain ranges having precipitous areas for use as escape terrain (Bleich and Holl 1982), and permanent water (Shackleton 1985). Frequently, these mountain ranges are isolated from each other (Schwartz et al. 1986, Bleich et al. 1990a). Wild sheep inhabiting desert environments are physiologically specialized in terms of water metabolism (Turner 1973).

Mountain sheep are gregarious but, for much of the year, males > 3 years-of-age live apart from females (i.e., they sexually segregate; Ober 1931, Geist 1971). Males and females aggregate during rut, which may extend for several months in desert environments (Welles and Welles 1961, Bunnell 1982). Because of this extended rut, desert-dwelling mountain sheep exhibit an extremely protracted

birthing season relative to their more northern conspecifics (Bunnell 1982, Rachlow and Bowyer 1991). Mountain sheep in highly productive habitats may breed as lambs and give birth as yearlings (Bleich 1986). Seegmiller and Ohmart (1982) demonstrated the existence of dietary differences between juvenile and adult female mountain sheep. Such allometric differences between adult males and females may explain the differential habitat use that commonly is observed.

Wolves (Canis lupus) may have been present in low numbers in desert habitats (Johnson et al. 1948), but extirpation of this canid from the southwestern United States has reduced its potential effects on wild sheep. Coyotes (Canis latrans), mountain lions (Felis concolor), and bobcats (Lynx rufus) are likely the most important predators of mountain sheep in desert environments (Kelly 1980). Coyote predation is widespread, and may be the major source of predator-related mortality for these desert-dwelling ungulates. Berger (1978) reported attempts of coyotes to kill mountain sheep, and Bowyer (1987) documented that coyotes in southern California may be effective predators of adult ungulates.

Hypothesized Explanations of Sexual Segregation, and Associated Predictions

Numerous hypotheses have been forwarded to account for sexual segregation in polygynous ungulates (Main and

Coblentz 1990, Miquelle et al. 1992, for reviews). Among these, 4 provide potentially logical explanations for sexual segregation in mountain sheep (Table 1); one (H_1) was developed with specific reference to mountain sheep (but has potential applicability to a large number of polygynous ungulates), and three (H_2 - H_4) may explain the segregation of sexes for bovids and cervids.

Critical tests of some of these hypotheses (Table 1) are difficult to obtain because of inherent problems in applying an hypothetico-deductive approach to ecological or evolutionary phenomena (Quinn and Dunham 1983); indeed, multiple causations of ecological events are common (Hilborn and Stearns 1982). Thus, I use the approach of multiple working hypotheses (Platt 1964). Predictions for each hypothesis in Table 1 will be compared with the results from this research. The 4 hypotheses may be falsified, based on comparison of empirical results with their predicted outcomes.

H_1: Sexual segregation occurs because males avoid competition with their mates and offspring. -- This hypothesis was proposed initially by Geist and Petocz (1977) to explain male mountain sheep inhabiting lower-quality ranges than those occupied by females. As McCullough (1979), Bowyer (1984), Verme (1988), and Miquelle et al. (1992) noted, however, it is difficult to explain why young

Table 1. Summary of hypotheses, predicted outcomes, and means of differentiating among hypotheses related to sexual segregation in mountain sheep.

Predicted Outcome	Hypotheses	Differentiation
Males on a lower quality diet than females	H_1 Males avoid competition with females to enhance their own fitness	Primarily class[a] III & IV males segregate from females
	H_4 Allometric differences lead to segregation	Class II-IV males segregate from females
	H_{4a} Males use low-quality resources unavailable to females but due to higher rumen volume: body ratio do better than females	Female movements result in segregation; percent of annual plants lower on male ranges, percent browse more on male ranges
	H_{4b} Females out-compete males for high quality resources	Primarily male movements result in segregation; percent of annual plants higher on female ranges
Males on a higher quality diet than females	H_2 Females evade predators by segregating	Females inhabit areas with more rugged terrain, or with fewer predators than do males

Table 1. (continued)

Predicted Outcome	Hypotheses	Differentiation
Male diets either of higher or lower quality than females	H_3 Differential water requirements cause spatial segregation	From H_1: Class II-IV males occur farther from water than females
		From H_4: Regardless of range quality, females and, particularly, females with young will be closer to water than class II-IV males

[a] Males are categorized according to age and size following Geist (1966, 1968).

males that typically do not mate should avoid competition with unrelated young, unless group selection is invoked. Indeed, Morgantini and Hudson (1981) pointed out that such behavior would result in males potentially reducing their own reproductive fitness. Further, group selection is unlikely to have affected the evolution or ecology of ungulates because of the unusual conditions necessary for it to operate (Williams 1966, McCullough 1979). Conversely, large, dominant males, which account for most mating in mountain sheep (Geist 1971), might benefit by spatial separation from females and young for selfish reasons, and this notion has not been adequately investigated. Moreover, the ideas of Geist and Petocz (1977) have been challenged on theoretical grounds rather than with empirical tests.

If males enhance their fitness by segregating from females and young, males would occur on poorer quality ranges than do females and their offspring. Additionally, males that segregate should be mature rams, and younger rams should not segregate because there would be no reproductive advantage gained. If males segregate to enhance their fitness, I predict that during sexual segregation: 1) Females inhabit ranges with better quality forage than do males; and 2) Large, dominant males spatially separate from females and young, but smaller, subordinate males are less likely to do so.

H_2: Spatial separation of the sexes occurs because mature males, owing to their larger body size and strength, are less susceptible to predators than smaller-bodied females and young, thereby allowing these males to exploit resources unavailable to smaller individuals. -- This hypothesis infers that mature males are able to use different ranges than females and immature animals, because males are larger and presumably less susceptible to being killed by predators. By differential use of these ranges, mature males are thought to maximize nutrient intake (King and Smith 1980, Geist 1982, Festa-Bianchet 1988a, McCullough et al. 1989, Main and Coblentz 1990), while females and young minimize predation risk (Ober 1931). McCullough (1979) discounted this idea because of the preponderance of adult male ungulates in the diet of many predators, and several investigators (Charles et al. 1977, Watson and Staines 1978, Staines et al. 1982, Bowyer 1984, Beier 1987, Clutton-Brock et al. 1987) reported that females occupied areas with better-quality forage than did males during segregation. Conversely, several other investigators (Wehausen 1980, Shank 1982, Festa-Bianchet 1986) documented that male mountain sheep occurred on higher-quality sites than did females. Thus, predator evasion might limit the distribution of females and young. These animals are particularly susceptible to predation (Curio 1976), and

often inhabit precipitous terrain, where forage quantity or quality is low, but where their ability to evade predators is enhanced.

If females and young segregate from males to evade predators, I predict that: 1) Females will obtain a lower-quality diet than mature males; 2) Females will occupy more rugged areas, with greater opportunities to evade predators than do these males; and 3) Relative numbers of predators will be lower on ranges primarily occupied by females than on ranges inhabited by mature males.

H_3: Females spatially segregate because of greater water requirements by lactating females, and young. -- Water requirements of lactating female ungulates are high (Short 1981), and this may be especially important in desert ecosystems. Bowyer (1984) ascribed sexual segregation for mule deer in a semi-arid environment to the dependence of females and their young on free water. The physiological burden of lactation may constrain females from venturing far from permanent sources of free water. Moreover, the relatively low water requirements of males compared to smaller-bodied females may allow them to occupy areas farther from summer sources of water, and thereby exploit resources unavailable to females.

If the constraints of lactation and body size contribute to sexual segregation, then I predict that:

1) Sexual segregation should be most pronounced immediately following the lambing season; 2) Females with young should occur closer to water sources than do males, or females without young; and 3) Because of their lower water requirements, mature males should occur farther from free water than young males during hot, summer months.

H_4: Allometric differences between males and females lead to differential use of food resources. -- McCullough (1979), Bowyer (1984) and Beier (1987) noted that adult males have lower food requirements per unit of metabolic body mass than adult females. Hence, males may be able to occupy habitats having poorer-quality forage, yet do as well nutritionally as females, because of the larger rumen-volume:body-mass ratio of males, and subsequent longer passage time for forage. Indeed, Illius and Gordon (1987) suggested that the differential scaling of metabolic requirements to body mass may cause ecological segregation of the sexes among grazing ungulates.

If allometric differences allow males to subsist on poorer-quality forage, yet do as well as females, I predict that: 1) Segregation will result primarily from the movements of female sheep from male ranges; 2) The percentage of annual plants, as well as forbs and grasses, will be lower on ranges occupied by mature male mountain sheep than on ranges occupied by females; and 3) The

percentage of shrub cover will be higher on ranges occupied by males than on ranges inhabited by females.

Females also might competitively exclude mature males from high-quality areas because males cannot effectively forage in areas with low availability of high-quality, but difficult-to-obtain, food. Because of differential scaling of metabolic requirements and incisor breadth (Illius and Gordon 1987), Seegmiller and Ohmart (1982) hypothesized that lambs would forage more selectively than adult females. Moreover, they concluded that adults, having higher energy and nutrient requirements/unit time, were precluded from consuming the smaller and more widely scattered food items of highest quality that were used by lambs. Seegmiller and Ohmart (1982) further suggested that adult male and female mountain sheep may be expected to have different diets, thereby explaining the spatial segregation observed between the sexes during certain seasons.

The supposed ability of larger animals to tolerate low-quality food, however, does not provide a rationale for seeking such foods, unless the supply of superior foods is limited. Where habitat segregation occurs between the sexes of ruminants, males often occupy poorer-quality habitats (e.g., Illius and Gordon 1987). Male red deer are less tolerant of low plant biomass than are females, and may be excluded from mutually preferred communities by indirect

(passive) competition (Clutton-Brock et al. 1987). Thus, Clutton-Brock et al. (1987) suggested that smaller grazing animals might tolerate lower levels of food availability than larger ones, and may progressively exclude larger species from mutually preferred areas by reducing standing crops to levels too low for larger animals (i.e., males) to graze economically.

If competition for forage between the sexes leads to sexual segregation, then I predict that: 1) Sexual segregation will result primarily from male movements from female ranges; 2) The percentage of annual plants, as well as forbs and grasses (i.e., high-quality foods), will be higher on ranges and in diets of females than for males; and 3) Mature males will occur at lower population densities than will females.

Objectives and Implications of the Research

The objectives of this research are to: 1) Describe and quantify sexual segregation in a population of desert-dwelling mountain sheep; and 2) Test 4 hypotheses (Table 1) that have been forwarded to explain sexual segregation among polygynous ungulates.

Hypotheses (Table 1) potentially explaining sexual segregation in ungulates are speculative (sensu Frankfurt 1987) and have been the subject of some controversy (Main and Coblentz 1990). No universal, single explanation for

this phenomenon may exist (Main and Coblentz 1990, Miquelle 1990), or information from a large number of ungulates, existing under diverse conditions, may be necessary to explain the adaptive significance of sexual segregation (Miquelle 1990). This research will add to the general knowledge of this complex phenomenon, and begin to elucidate the proximate and ultimate causes of sexual segregation in mountain sheep, with general applicability to other ungulates.

An understanding of how male and female mountain sheep partition space and resources, and the effects of sexual segregation on recruitment of young, is essential for expanding our knowledge of sexual selection in polygynous ungulates, and for the future conservation of mountain sheep. For example, much of our understanding of why the sexes segregate comes from cervids (which tend to be more r-selected than mountain sheep), or from mountain sheep populations occurring at more northern latitudes (Oldemeyer et al. 1976, Tilton and Willard 1982, Ashcroft 1986, Fairbanks et al. 1987, Wakelyn 1987).

Likewise, knowledge of why the sexes remain apart outside the mating season is necessary to understand habitat selection or to advance modeling of population dynamics for ungulates. For instance, McCullough (1979) documented that sexual segregation resulted in a significant inverse

relationship between the density of female white-tailed deer and the rate at which young were recruited into the population, whereas the correlation between male density and recruitment rate provided a weaker fit. This outcome ostensibly occurred because the distributions of females and young overlapped throughout the year (thereby increasing competition for limited resources). In contrast, competition of young with mature males was minimal, except during rut, because of their disjunct distributions (McCullough 1979).

Information for mountain sheep inhabiting desert environments is especially important to understand the complex habitat and nutritional relationships exhibited by these large mammals. The results of this research will have important implications for habitat conservation (e.g., Bleich et al. 1990a) and for the future of these large, specialized ungulates. Moreover, these results will bear heavily on the processes used in selecting sites on which to reestablish populations of mountain sheep (Bleich et al. 1991). Indeed, the findings presented herein will provide an important theoretical framework for understanding sexual segregation, and shape management and conservation strategies for desert-dwelling mountain sheep far into the future.

STUDY AREA

Location, Topography, and Geology

Old Dad Mountain, Cowhole Mountain, the Kelso Mountains, and the Marl Mountains are located approximately 30 km southeast of Baker, San Bernardino Co., California (Fig. 1). The surrounding area includes expansive lava beds located northeast of the Kelso Mountains, and a large area of relatively stable sand dunes, the Devils Playground, west of Old Dad Mountain. The study area encompassed 1,265 km^2.

Nearby ranges include the Bristol, Soda, and Providence mountains. With the exception of the Bristol Mountains, movements of mountain sheep between Cowhole Mountain, Old Dad Mountain, the Kelso Mountains, the Marl Mountains, and these other ranges have been observed.

Old Dad Mountain reaches an elevation of 1,308 m, and the maximum elevation of the Marl Mountains is 1,387 m; Kelso Peak has an elevation of 1,466 m. Within the study area, the desert floor gradually gains elevation from west to east, and intermountain areas range from approximately 300 m at the base of Cowhole Mountain to about 1,750 m near the Providence Mountains, southeast of the Marl Mountains.

Old Dad and Cowhole mountains are composed mostly of limestone, and the Kelso and Marl mountains are primarily of

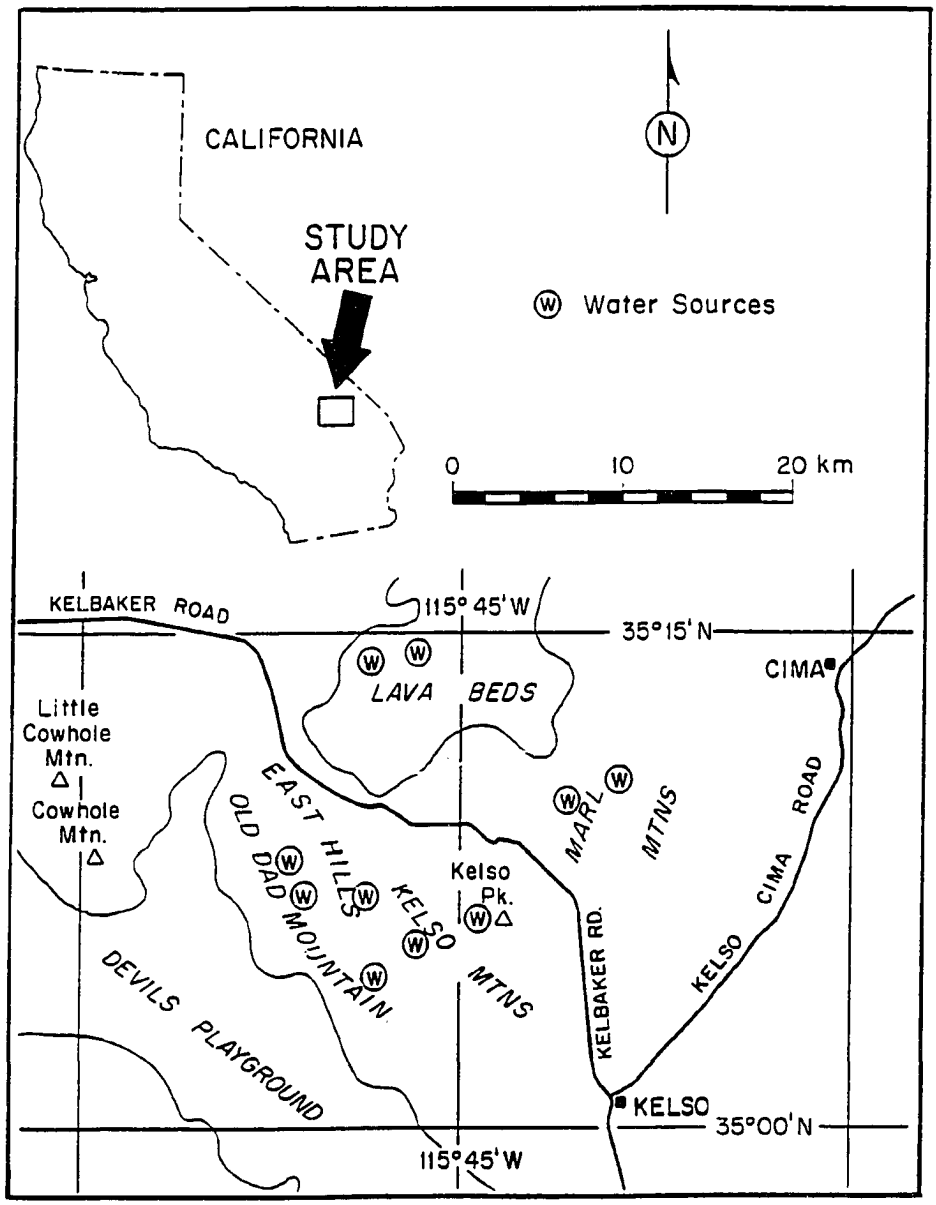

Fig. 1. Study area in San Bernardino Co., California showing the desert mountain ranges inhabited by mountain sheep. Females occurred primarily at Old Dad and Cowhole mountains, and males mostly in the East Hills and Marl and Kelso mountains during sexual segregation.

granitic origin. South and east of Old Dad Mountain, major ridges of volcanic origin occur. The geology of Old Dad Mountain and vicinity has been described in detail by Barca (1966), Dunne (1977) and Curry and Resigh (1983).

Climate

The study area is located in an extremely arid portion of the Mojave Desert. Daytime maxima in summer normally exceed 38^{o} C, and winter temperatures below freezing are not uncommon (Weaver et al. 1969). Annual precipitation in the vicinity of the study area averages 8 cm, with about 50% falling as summer thundershowers (Fig. 2; Freiwald 1984). Thundershowers are extremely localized, and heterogeneity of rainfall likely has a strong but spatially restricted influence on forage quantity and quality for mountain sheep.

Water Sources

Ten water sources used by mountain sheep are present in the study area (Fig. 1); availability of free water at the 6 natural springs is unpredictable. Four artificial sources provide water on a year-round basis (Bleich and Pauli 1990), and are used heavily by mountain sheep, particularly during summer (Bleich 1983a, Bleich et al. 1987, Jaeger et al. 1991). Two ephemeral springs in the volcanic badlands receive only occasional use by mountain sheep.

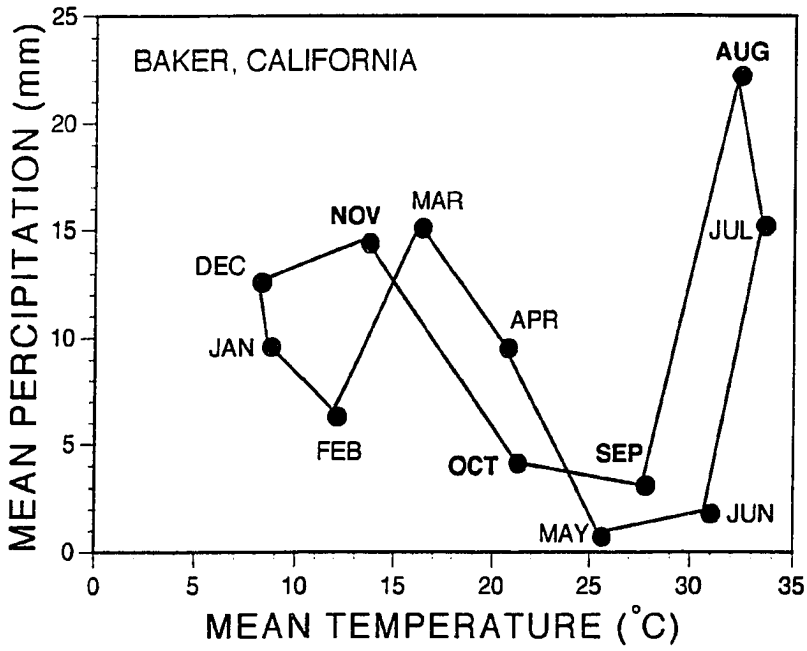

Fig. 2. Thermograph of monthly precipitation and temperature 30 km NW of Old Dad Mountain, San Bernardino Co., California, 1983-89. Months in bold letters indicate the period of sexual aggregation (rut) for mountain sheep.

Flora

Martens and Baldwin (1983) described 6 primary vegetation communities in the study area (Fig. 3; Appendix A): Creosote bush scrub (CBS), wash scrub (Wash), Yucca-Ephedra scrub (YES), partially stabilized dunes (PSD), stabilized dunes (SD), and rupicolous scrub (RS). A seventh vegetation type, intermediate in characteristics between CBS and YES, that occurs between the upper limits of CBS and the lower limits of YES, is the transition zone (TZ). A primary characteristic of the TZ is its remarkably dissimilar vegetation on different slope aspects. In general, north-facing slopes support vegetation similar to YES; all other aspects within the TZ have vegetation typical of CBS (Martens and Baldwin 1983).

In the eastern portion of the study area, YES, CBS, and TZ vegetation associated with lava flows were identified as such (Fig. 3). Areas almost devoid of vegetation also occur east of Old Dad Mountain; these areas were identified as "cinder" for descriptive purposes. I grouped SD and PSD vegetation into a single habitat type termed Dune. A limited amount of vegetation identified as Pinyon Pine occurs in the Providence Mountains.

Fauna

With the possible exception of wolves (Johnson et al. 1948), the study area contains a full complement of large

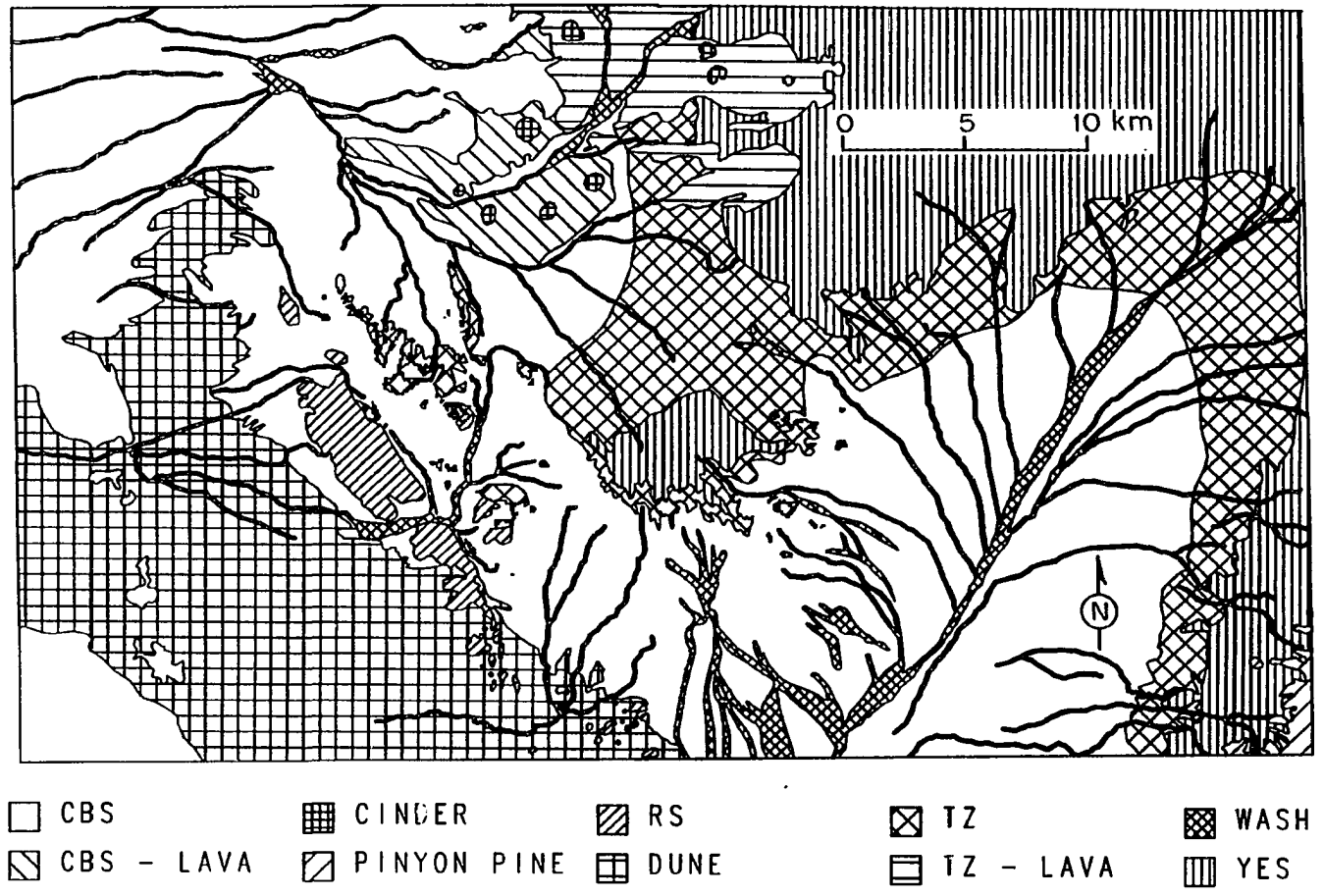

Figure 3. Vegetation types in the Old Dad Peak/Kelso Mountains study area, San Bernardino County, California.

mammalian carnivores, including bobcats, mountain lions and coyotes; only coyotes are common. Mountain lions were not reported in the eastern Mojave Desert by Johnson et al. (1948). These large felids may have colonized this area following the introduction of mule deer in 1948 (Longhurst et al. 1952).

Mule deer occur only infrequently in the study area; other sympatric ungulates include domestic cattle and numerous feral asses (> 100 animals). Three livestock allotments encompass the study area, and cattle are grazed during spring, autumn and winter in the Kelso and Marl mountains, and on sandy areas south of Old Dad Mountain (Sorensen 1982, 1983, 1984).

Approximately 160 female and 205 male mountain sheep inhabit the study area (Jaeger et al. 1991), and represent part of a larger metapopulation (Schwartz et al. 1986, Bleich et al. 1990a) occupying the eastern Mojave Desert. Based on the estimates of Jaeger et al. (1991) and the distribution of mountain sheep (this paper), males occurred at a slightly higher overall density (0.32/km^2) than did females (0.27/km^2). This difference in density is due, in part, to translocations of sheep from the study area (Bleich et al. 1990b).

Human Influences

Old Dad Mountain has been the subject of intense mineral exploration, but only one mine currently is in operation, and is not known to affect the sheep population adversely. A large cinder mine also operates in the lava beds; likewise, that operation is not known to affect sheep.

A network of roads was constructed to support historical, large-scale mining in this area; a lightly used, nonmaintained dirt road bisects the study area along a powerline corridor that extends from west to east, and Kelbaker Road, running between the desert hamlets of Baker and Kelso, traverses the study area on a north-south axis (Fig. 1). The Government Road, constructed during the mid-1800's (Casebier 1983), currently receives heavy recreational use.

Hunting occurs for lagomorphs, upland game birds, mule deer, and predators during the regular hunting seasons; some commercial trapping of furbearers also occurs. Since 1987, that portion of the study area west of Kelbaker Road has been open to limited hunting of mountain sheep, and a total of 25 mature males have been harvested through the 1991 hunting season (Bleich et al. 1992a). From 1983-1989, 172 mountain sheep (46 males, 126 females) were removed from the study area for translocation to other historical ranges (Bleich et al. 1990b).

METHODS

Capturing Mountain Sheep

From September 1986 to June 1990, 44 mountain sheep (27 males, 17 females) were captured and fitted with telemetry collars incorporating mortality sensors (Telonics, Mesa, Ariz.; Bleich et al. 1990c). Most individuals were captured using a hand-held net gun (Krausman et al. 1985, Jessup et al. 1988) fired from a Bell 206B-III helicopter flown by a pilot experienced in that procedure (Bleich 1983b); two animals were captured by driving them into a net (Beasom et al. 1980). All aspects of animal handling complied with acceptable field methods adopted by the American Society of Mammalogists (Ad Hoc Committee on Acceptable Field Methods 1987), and were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks.

Radiotelemetry

An attempt was made to locate telemetered animals once each week from 1 October 1986 through 31 December 1990 using a fixed-winged aircraft (Cessna 185) flown by an experienced pilot, but inclement weather precluded strict adherence to that schedule. The aircraft was equipped with a directional "H-antenna" (Telonics, Mesa, Ariz.) on each wing strut, and locations of telemetered animals were determined in a manner

similar to that described by Krausman et al. (1984). Geographic coordinates incorporated necessary corrections (Patric et al. 1988) and were estimated with a LORAN-C navigation system.

Aerial-telemetry locations were accurate within about 4 ha of actual locations (Krausman et al. 1984; M. C. Nicholson, unpubl. data). Such accuracy was adequate for this investigation because habitat types occurred over relatively homogeneous, large areas. Additionally, errors for these locations were small relative to the home ranges of sheep ($\geq$ 5 km^2). The locations of collared mountain sheep were visually confirmed during 14 flights, and they coincided with the estimated telemetry locations on all occasions. Moreover, the carcasses of 9 telemetered animals were retrieved from locations determined by aerial telemetry, further confirming accuracy of this technique.

Aerial Surveys

Data from 20 helicopter surveys conducted from May 1981 to December 1990 were used to determine periods of sexual segregation and aggregation. A pilot and 3 observers experienced in those procedures (Bleich 1983b) participated in all surveys. The study area was partitioned into 5 survey polygons (26-83 km^2), and each was searched systematically (Bleich et al. 1990d) at an intensity of approximately 2.5 min/km^2. Each observation of a mountain

sheep was plotted on USGS 15-min (1:62,500) topographic maps, and these locations were converted to Universal Transverse Mercator (UTM) Grid coordinates (Monmonier and Schnell 1988). Marked animals seen during these surveys also were recorded, as were other ungulates and predators.

Ground Observations

Ground observations were made from June 1987 to December 1990, and these data also were used to define periods of sexual segregation and aggregation. Because the intent of ground surveys was to obtain data on lamb recruitment for concurrent studies (Wehausen 1988, 1990, 1992, Jaeger et al. 1991), these efforts were concentrated in areas used primarily by females, young males, and lambs. Observations were recorded on 15-min USGS topographic maps and later converted to UTM coordinates.

Time-Lapse Photography

Time-lapse photography (Davis and Bleich 1980, Jaeger et al. 1991) was used to record sheep at water sources. Photographs were taken every 60 s during adequate daylight, and cameras were positioned to facilitate the correct classification of sheep (Jaeger et al. 1991). Cameras operated almost constantly during June through September 1988-89, for 4 days/mo during October 1989 through May 1990, and briefly during summer 1990.

Each frame of film was analyzed using the "groups/frame" method of Jaeger et al. (1991), to help insure that samples were independent. These data supplemented those obtained during ground and aerial sampling to determine periods of sexual segregation and aggregation, as well as to assess the relative abundance of carnivores at water sources.

Group Composition

For statistical purposes, a group consisted of $\geq$1 mountain sheep. During aerial surveys, animals $\leq$ 100 m from each other were considered to be in the same group, because the noise associated with the aircraft may have caused groups to begin fragmenting before they were observed. During ground sampling, undisturbed animals were placed in the same group if they were $\leq$ 50 m from one another (Siegfried 1979) or appeared to be aware of the presence of other nearby conspecifics and moved cohesively. Sheep in the same photograph were considered to be a social group.

Each sheep was classified (Geist 1968) as follows: Class I, II, III, and IV males; yearling females; adult females ($\geq$ 2 years-of-age), and lambs (individuals of either sex, < 1 year-of-age). Class I males were 1-2 years-of-age, and are referred to as yearling males. Class II males generally were 2-3 years-of-age, and are referred to as young males. Class III and IV males were $\geq$ 4 years-of-age,

and were termed mature males. All males ≥ class II were considered to be adults.

Five major social groups (sensu Hirth 1977) were recognized. Female groups contained ≥ 1 adult female, but could include yearlings or lambs. Male groups contained ≥ 1 class II, III or IV male, but could also include class I males; male groups never contained females or lambs. Mixed groups contained at least one adult male and one female but could also include class I males, and lambs. Yearling groups consisted of yearlings of either sex, and rarely included lambs. Lamb groups contained only young of the year.

Vegetation Sampling

During April 1990, I quantified vegetation using 92 randomly located step-point transects (Evens and Love 1957; as modified by Bowyer and Bleich [1984]). I recorded a cover "hit" if the point (<1 mm in diameter) fell within the canopy of a shrub or on a stem or leaf of a plant; a frequency hit was recorded if the point contacted the stem of any plant where it entered the ground. Points not recorded as frequency or cover for plants were tallied as bare ground (including rocky substrates). Each transect contained about 300 step-points (recorded every other step--2 m apart) that were used to calculate percent cover and frequency for that transect. Adequate sample size for each

vegetation type was determined by cumulatively summing the percent cover of the 5 most common plant species across transects, until the means stabilized (Kershaw 1964:29). Annual vegetation also was sampled during April 1991 and April 1992. Plant nomenclature follows Munz (1974).

At the beginning, middle, and end of each step-point transect, horizontal cover was estimated using a cover-pole (Griffith and Youtie 1988). Cover-poles were 2 m in height, and divided into 8 bands, each 25 cm in length. An observer recorded cover of the pole from 4 directions from a distance of 15 m. These directions were at right angles to one another, and the initial direction was selected randomly. The percentage of each band not visible from the 4 directions was estimated. The average cover for each 1-m length of the cover pole was then calculated, using the 16 values estimated for that increment of the pole. Horizontal cover for each vegetation type is expressed as the mean percent of the pole not visible from > 1 m, and from < 1 m above the ground. To quantify the role of geomorphic features in determining horizontal cover, I recorded those instances in which rocks, or changes in slope, affected cover as measured by the pole; these were expressed as the mean number of occurrences per 1-m increment of the cover pole for each vegetation type.

Habitat Characteristics

A Geographic Information System (GIS) was used to create a coverage of vegetation types. A commercially available digital-elevation model (SoftWright, Aurora, Colo.) was used with the triangulated irregular network (TIN) module of ARC/INFO (Environmental Systems Research Institute, Redlands, Calif.) to create a 3-dimensional surface model of the study area, and was later converted to a 2-dimensional polygon coverage. From the TIN, the elevation, slope, and aspect of ground, aerial, and telemetry locations of mountain sheep were determined (Bleich et al. 1992c). Additionally, the distance from each sheep location to the nearest available source of water was calculated.

An index of terrain ruggedness was created by converting the 3-dimensional surface model into a coverage of 12-m contour lines. Grids, each 1 km by 1 km, were overlaid on the study area, and the number of arcs forming the contour lines within each square was tallied. Using the GIS, this index of ruggedness was associated with each sheep location according to the grid square in which that location occurred. Because of the large size of the grid cells, the total number of contour lines occurring within each cell provided an indirect measure of overall topography; the more

rugged the terrain, the greater the number of contour lines that occurred in that cell.

Separate coverages were created for vegetation type, slope, and aspect, based on minimum-convex polygons created from telemetry data for periods when the sexes were segregated and aggregated, as well as for year-round distributions of sheep. Each of these polygons was then enlarged with a buffer of 1,000 m, and the resulting polygons were used to determine the availability of 9 slope categories, and 12 aspect classes within each buffered area. Using the GIS, new coverages containing information on slope and aspect were created, and summary information concerning the availability of these variables was generated. In a similar manner, new vegetation coverages were produced for each buffered minimum-convex polygon. From these coverages, summary statistics concerning the availability of vegetation types were generated.

A set of telemetry locations corrected for autocorrelation (Solow 1989) was developed for each telemetered animal using BLOSSOM statistical software (Slauson et al. 1991). The resulting point locations were used in subsequent analyses of habitat selection (Neu et al. 1974, Heisey 1985); each animal contributed a near equal number of observations for these analyses.

Diet

Whenever possible, fresh fecal pellets ($n \geq 25$) were collected monthly from July 1987 to June 1990 from individuals of known sex and age; otherwise feces were obtained from female or male groups. Sampling was stratified by those parts of the study area used predominantly by males or females during sexual segregation. During rut, male sheep regularly occurred in areas otherwise used by females, and fecal samples were collected from males as they were encountered. As samples were collected, they were placed in paper bags and air-dried until further processing was possible.

Diet composition was analyzed by a technician familiar with diets of desert sheep (Krausman et al. 1989, Miller and Gaud 1989) at the Forage Analysis Laboratory, University of Arizona, using the method of Sparks and Malechek (1968). Three slides per pellet group were prepared (Holechek and Vavra 1981), and the frequency of a species, appearing in each of 20 randomly selected microscope fields per slide, was determined (i.e., 60 fields/pellet group).

To avoid artificial inflation of sample sizes (Hurlbert 1984), I calculated the average frequency with which a forage species appeared on each slide, and converted these values to relative particle density (Fracker and Brischle 1944, Sparks and Malechek 1968) for each sample (pellet

group). Thus, the number of monthly samples for each sex was equal to the number of pellet groups examined. Mean particle density was then calculated by summing the relative density for each forage species, and dividing the result by the total number of samples. I categorized plants as annuals, perennial forbs, perennial grasses, woody perennials, and succulents (cacti).

Absolute determination of sheep diets from microhistological analysis may be problematical because of differential digestibility of some forages (Fitzgerald and Waddington 1979). I assume, however, that this technique provides an index to diets of male and female sheep. Indeed, the proportion of fragments of some plants may remain relatively constant when passing through the digestive tract (Todd and Hansen 1973).

Diet Quality

Fecal crude protein (FCP = fecal nitrogen x 6.25) usually was determined for $\geq$ 5 individual pellet groups/sex/month, using micro-Kjeldahl digestion, at the Wildlife Habitat Laboratory, Washington State University. Use of FCP to measure quality may be problematic when diets are composed primarily of species high in protein-complexing phenolics (Robbins et al. 1987). Nonetheless, FCP has been correlated positively with dietary nitrogen for a number of ungulates (Gates and Hudson 1979, Johnson et al. 1987,

Leslie and Starkey 1985, 1987, Mubanga et al. 1985, Renecker and Hudson 1985). Further, recent studies have documented the effectiveness of FCP for indexing seasonal differences in diet quality (Beier 1987, Pletscher 1987), as well as variation in range condition (Erasmus et al. 1978, Hodgman and Bowyer 1986). This method has been especially useful as an index of diet quality for mountain sheep (Hebert 1973, Wehausen 1980, Seip and Bunnell 1985, Festa-Bianchet 1988a, Rachlow and Bowyer in press).

Forage Quality

Percent *in vitro* dry matter digestibility (IVDMD), crude protein (CP), and moisture content were determined on a monthly basis for 20 plant species eaten by mountain sheep (Bleich et al. 1992b). Samples were collected from portions of the study area inhabited almost exclusively by either sex outside rut. Data from Bleich et al. (1992b) were re-analyzed to evaluate potential differences in IVDMD, CP, and moisture content for these forage species.

Relative Abundance of Predators

Relative abundance of potential predators was estimated based on three independent measures: 1) Predator feces on transects; 2) Time-lapse photography at water sources; and 3) Aerial surveys. Data were recorded from areas used predominantly by mature males or females.

Belt transects (n = 93) were sampled coincident with the routes hiked ($\bar{X}$ = 8.0 km, SD = 3.0) when conducting surveys of sheep during 1987-88. I tallied all fresh (unbleached) predator feces within 1 m either side of a line of travel (Pelton 1972, Hone 1988); no transects were resampled during this investigation. Predator feces were identified according to characteristics described by Murie (1954) and Danner and Dodd (1982). Sparse ground cover in this arid environment reduced the likelihood that scats were overlooked. Relative abundance is expressed as scats/ha.

Time-lapse photography was used to record daytime visits at waterholes by coyotes, bobcats, and two species of foxes (*Urocyon cinereoargenteus* and *Vulpes macrotis*); no mountain lions were recorded. Because foxes and juvenile coyotes sometimes were not distinguishable, these carnivores were pooled into a category termed "other." Bobcats, as well as adult coyotes, may have been placed in this category occasionally.

Time-lapse cameras at 2 water sources (Kelso guzzler and Jackass Spring) were located in areas used predominantly by male mountain sheep; 2 others (Old Dad and Kerr guzzlers) were in areas used predominantly by females (see **Time-Lapse Photography**). Relative abundance of predators at water sources was expressed as the number of predators (by species)/10,000 frames of film.

I also recorded predators in sampling polygons (Bleich et al. 1990*d*) during > 100 h of helicopter surveys (*n* = 20). Abundance was expressed as predators/survey hour/km^2 x 1000.

Predator Food Habits

Predator feces (scats) were collected from transects conducted for that purpose (*n* = 60), and when scats were encountered during other field activities (*n* = 60). Laboratory analyses of prey remains in predator feces followed the procedures of Bowyer et al. (1983). Hair of ungulates was identified by its characteristic morphology (Mayer 1952). In the field, carcasses of mountain sheep were carefully examined and, if evidence was available, the probable predator was identified according to the criteria of Shaw (1983) or Woolsey (1985).

Body Mass of Sheep

Body mass (±0.5 kg) was determined using a platform scale, and chest girth was measured to the nearest 1 cm for 172 mountain sheep captured in the study area from 1983 to 1989 (Bleich et al. 1990*b*). Age of each animal was estimated using patterns of incisor replacement (Deming 1952) and horn-growth rings (Geist 1966).

Statistical Analyses

Statistics used in this study include both multivariate and univariate tests. I examined assumptions of each test and transformed data (log, SIN, COS, SIN^{-1}, rank) as

necessary to meet these criteria. In some instances, I substituted the appropriate nonparametric test (e.g., Mann-Whitney, Kruskal-Wallis, and Friedman tests, Spearman correlation; Zar 1984) for *t*-tests, analyses of variance, or regression. Proportions were examined with the *Z*-test; the *G*-test was used for most categorical analyses (Zar 1984). The analysis used is clearly indicated in each section of the results, although some additional information on analyses of selection and independence of samples is dealt with under appropriate sections in the **METHODS**. SYSTAT (Wilkinson 1988) or BMDP (Dixon 1985) was used for most analyses. In all cases, an $\alpha = 0.05$ was adopted.

RESULTS

Sexual Dimorphism

Desert-dwelling mountain sheep exhibited extreme sexual dimorphism in body mass (Table 2). Class III and IV males were about 1.5 times heavier than adult females, class II males about 1.2 times heavier; yearling males and male lambs were also slightly larger than their female counterparts.

Social Aggregation and Segregation

I categorized groups of mountain sheep observed from the ground (n = 548) and air (n = 869) as mixed, female, male, yearling, and lamb. A significant positive correlation (r_s = 0.68, P < 0.05, n = 11) between the percent of mixed groups during aerial and ground sampling indicated that this monthly pattern was similar; hence, results of those surveys were combined (Fig. 4).

A significant difference (Z = 2.6, P = 0.004) was evident between the proportion of mixed groups occurring from August to November ($\bar{X}$ = 18.4%, SD = 11.1%) and from December to July ($\bar{X}$ = 3.3%, SD = 2.0%) (Fig. 4). Indeed, most mixed groups (73.5%) occurred from August to November; consequently, the season of sexual aggregation was defined as that period, and the season of sexual segregation was

Table 2. Degree of sexual dimorphism, as reflected in body mass and girth, for sex and age classes of mountain sheep, San Bernardino Co., California, 1983-89.

	Males							
	Class III and IV (n = 16)		Class II (n = 8)		Yearling (n = 12)		Lamb (n = 11)	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Body mass (kg)	70.2	12.0	58.5	8.1	40.7	9.4	27.8	8.5
Girth (cm)	98.0	8.2	92.2	5.0	83.9	6.9	75.3	11.4
Age (yrs)	5.3	1.5	2.8	0.5	1.0	0.0	<1.0[a]	--

	Females					
	Adult (n = 90)		Yearling (n = 22)		Lamb (n = 14)	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Body mass (kg)	47.9	6.0	35.0	5.9	26.4	6.0
Girth (cm)	89.0	4.2	78.3	5.9	72.5	6.9
Age (yrs)	5.1	2.2	1.0	0.0	<1.0[a]	--

[a] Most lambs were captured in December, and were ca. 8-10 months-of-age.

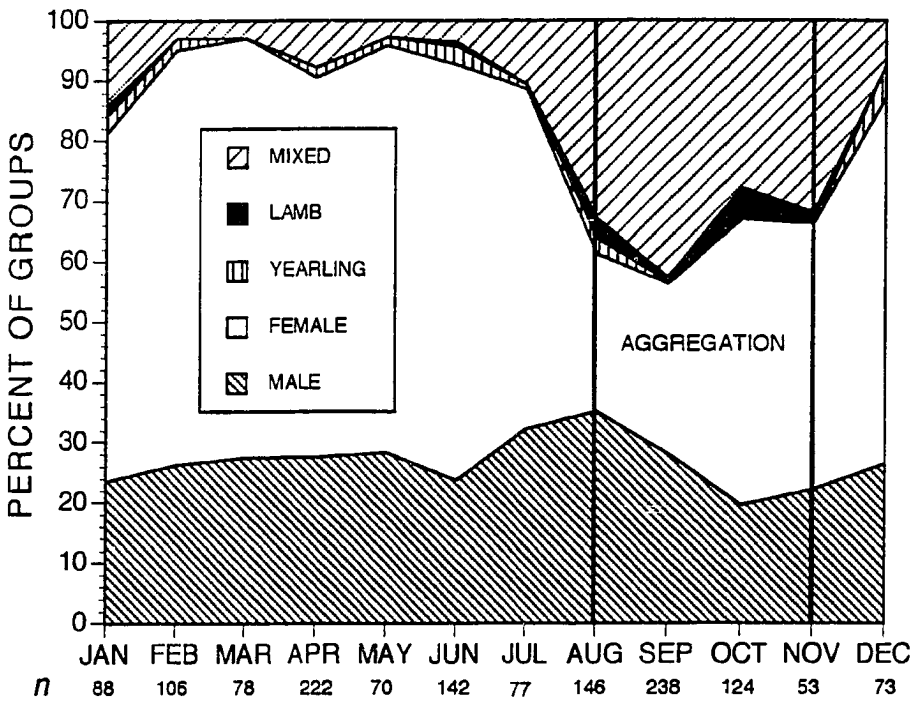

Fig. 4. Percent of social groups for mountain sheep based on ground and aerial sampling, San Bernardino Co., California, 1981-90. The period of sexual aggregation is the rut.

from December to July (Fig. 4). Likewise, a total of 221,854 frames of time-lapse camera film at water sources used by both sexes indicated that mountain sheep (n = 361 groups) occurred twice as often in mixed groups during aggregation (14%) as during segregation (7%). Significant differences in the percent of mixed groups between these periods occurred from July 1988 to June 1989 (G = 9.13; 3 df; P = 0.03), as well as from July 1989 to June 1990 (G = 18.26; 3 df; P = 0.002).

Because some mixed groups (Fig. 4) contained males no larger than class II, and these males are important in testing hypotheses concerning sexual segregation (Table 1), I further examined how these males associated with other sheep (Fig. 5). Significant differences existed in the percent of class II males associating with groups containing females, other young males (class I and II), mixed groups with mature males (class III and IV), and groups containing only mature males (G = 22.44; 3 df; $P < 0.001$). During segregation, class II males commonly associated with mature males, but much less so with groups containing females. During aggregation, however, class II males were observed often with females, especially in those groups containing mature males (Fig. 5).

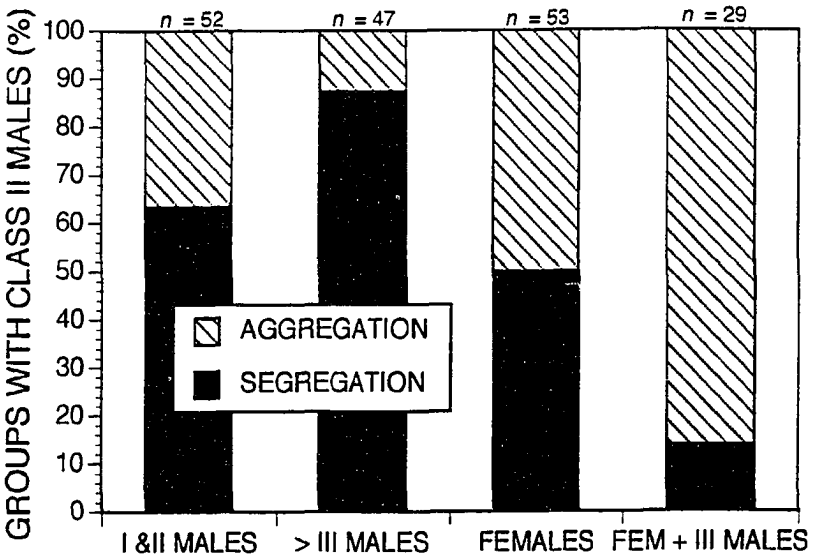

Fig. 5. Associations of class II males (as determined by ground and aerial observation) in other social groups of mountain sheep, during periods of aggregation and segregation, San Bernardino Co., California, 1981-90.

Group Size

A 3-way ANOVA (1, 1,358 df) indicated that group size of mountain sheep varied by survey type (F = 24.10, P < 0.001), periods of segregation and aggregation (F = 99.00, P < 0.001), and type of social group (F = 26.60, P < 0.001) (Fig. 6). Overall, mixed groups ($\bar{X}$ = 5.3, SD = 3.6, n = 207) were larger than female ($\bar{X}$ = 3.4, SD = 3.1, n = 738), male ($\bar{X}$ = 1.9, SD = 1.5, n = 424), yearling ($\bar{X}$ = 1.9, SD = 0.4, n = 31 and lamb ($\bar{X}$ = 1.9, SD = 1.5, n = 17) groups.

Spatial Distribution

Whether males joined females during sexual aggregation or vice versa is an important consideration (Table 1). On an annual basis, approximately 70% of the observations of telemetered female mountain sheep occurred at Old Dad Mountain (Fig. 7). No significant difference (G = 4.06; 3 df; P = 0.26) existed in the distribution of females between segregation and aggregation. Female mountain sheep remained primarily in those areas typified by steep, open terrain. In contrast, significant differences (G = 34.82; 3 df; P < 0.001) occurred in the distribution of males between segregation and aggregation (Fig. 7). Males moved to join females during aggregation, and then returned to the East Hills, and the Kelso and Marl mountains during segregation (Figs. 1, 7).

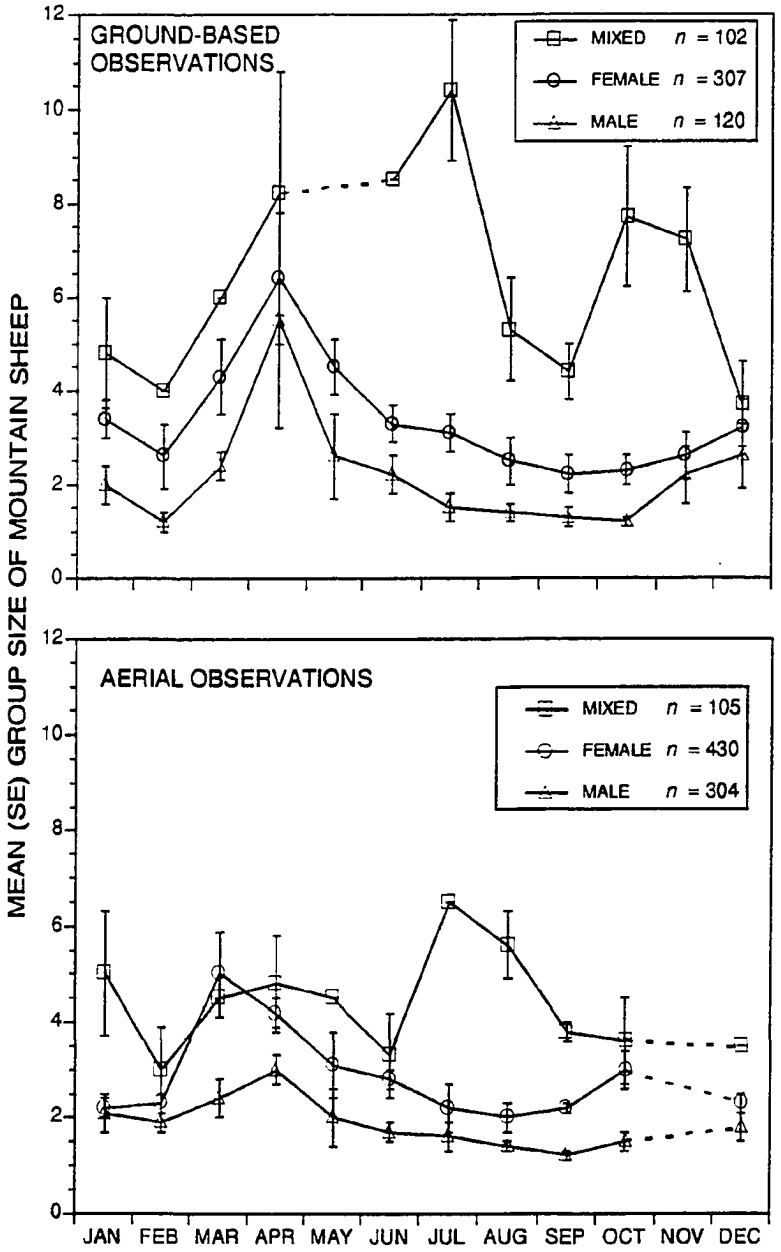

Fig. 6. Mean size of mixed, female, and male groups of mountain sheep, San Bernardino Co., California. Ground-based observations were made during 1984-90; aerial observations are from 1981-90.

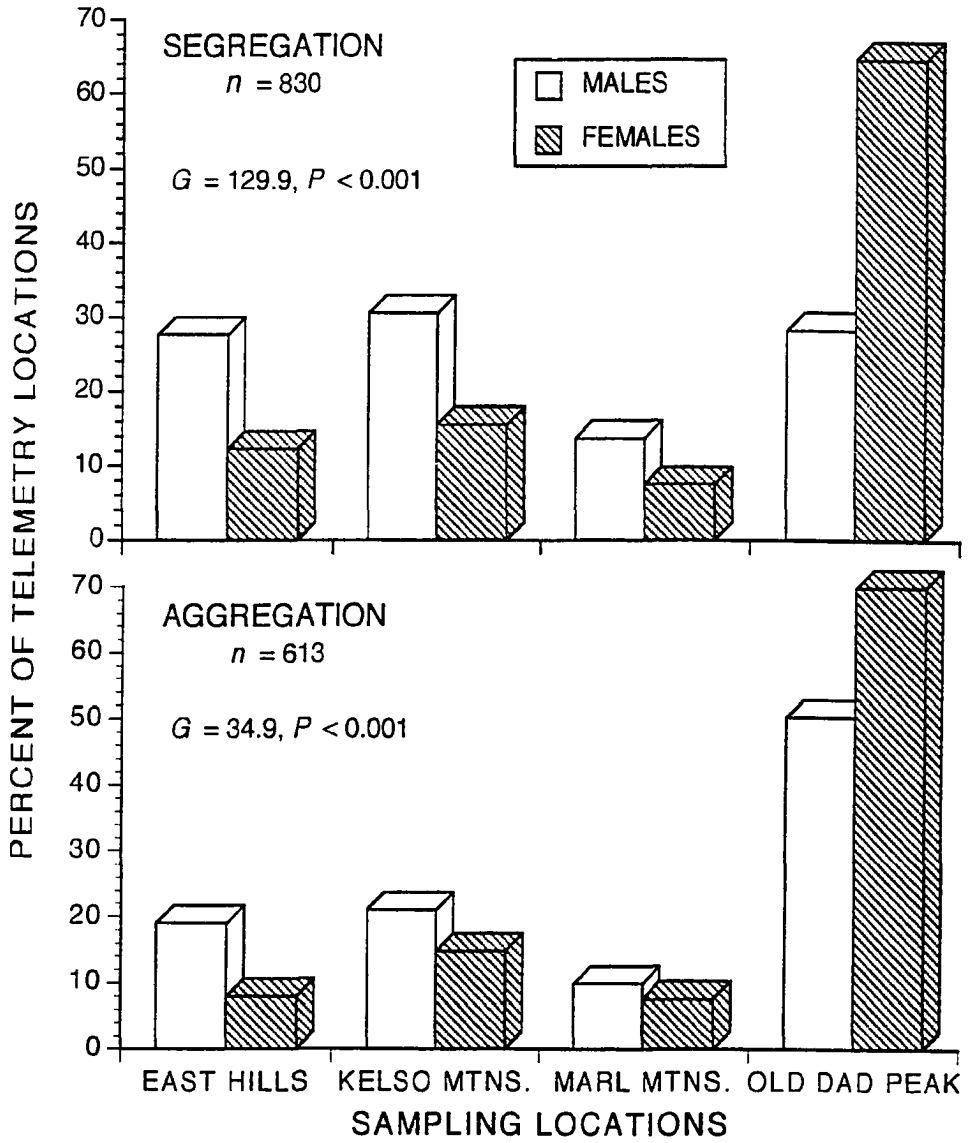

Fig. 7. Percent of telemetry locations of male and female mountain sheep on various ranges, San Bernardino Co., California, 1986-90. G-statistics are comparisons of males and females within periods. Note the shift in the distribution of males to Old Dad Mountain during aggregation.

Composition of Plant Communities

To examine the potential role of vegetation in the way males and females used habitat, I analyzed the composition of 6 vegetation types (Table 3, Fig. 8, Appendix A). Percent ground cover of nonwoody vegetation (annual plants, perennial forbs, perennial grasses), succulents, and perennial shrubs, was significantly different among vegetation types ($\underline{X}_r^2$ = 6.78, 2 df, $\underline{P}$ < 0.05). Percent ground cover of nonwoody vegetation was greater in YES and TZ (Fig. 8) than in RS, a vegetation type used predominantly by female mountain sheep. These data indicate greater availability of annual plants, perennial forbs, and grasses in areas used by males than those inhabited by females. Similarly, percent ground cover of woody shrubs also was greater in YES and TZ than in RS, suggesting that vegetation may obscure visibility more in areas used predominantly by males, and that shrubby forages likewise are more abundant in those areas (Fig. 8).

Annual vegetation potentially is an important source of high-quality forage when mountain sheep are segregated by sex. I compared the cover and frequency of annual plants in CBS, YES, and RS during April for 3 consecutive years (Fig. 9). No significant differences existed between mean cover of annual plants (Kruskal-Wallis) test, $\underline{X}^2$ = 5.23, 2 df, $\underline{P}$ = 0.15) among these vegetative types during 1990, but such

Table 3. Use of slope characteristics and distance to water for male and female mountain sheep based on telemetry locations, San Bernardino Co., California, 1986-90.

Habitat Characteristics	Males					Females				
	Segregation (n = 445)			Aggregation (n = 333)		Segreation (n = 414)			Aggregation (n = 296)	
	$\bar{X}$	SD	P[a]	$\bar{X}$	SD	$\bar{X}$	SD	P[a]	$\bar{X}$	SD
Distance to water (m)	3,091[S]	1,760	NS	3,087[A]	2,194	2,449	2,190	NS	2,481	2,016
Elevation (m)	1,012[S]	177	*	957	186	961	197	NS	943	204
Slope (%)	14[S]	12	*	17[A]	14	25	11	NS	24	16
Ruggedness (index)	13[S]	8	*	16[A]	10	24	13	NS	2.2	12
E-W aspect (SIN°)	0.03	0.71	NS	0.01	0.70	0.11	0.72	NS	0.07	0.72
N-S aspect (COS°)	-0.03	0.70	NS	-0.05	0.71	-0.04	0.69	NS	0.01	0.68
Openness (ranked 1-6, 1 most open)	3.9[S]	1.1	*	3.6[A]	1.2	3.2	1.3	NS	3.1	1.4

[a] P-values are from within sex ANOVAs with Bonferroni corrections; NS = $P > 0.05$, * = $P \leq 0.05$. [S] indicated that males differed ($P \leq 0.05$) from females during segregation, and [A] indicates the same for aggregation using this identical statistical approach.

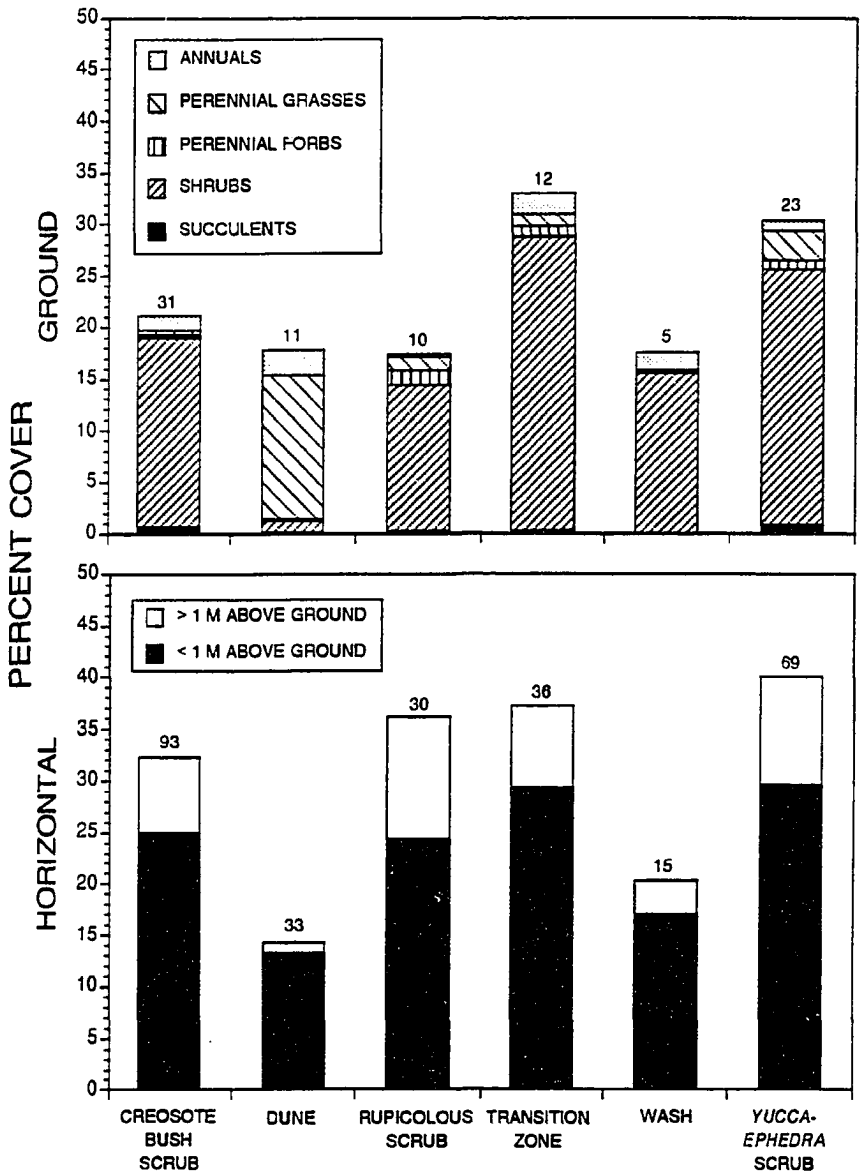

Fig. 8. Percent ground cover of vegetation classes composing habitat types, and the horizontal cover (which obscures visibility) in those types, San Bernardino Co., California, April 1990.

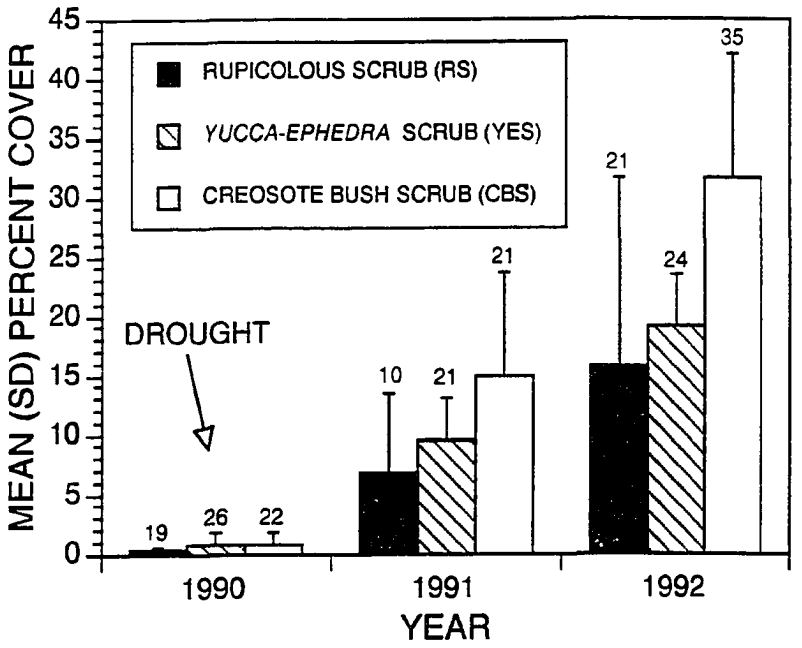

Fig. 9. Percent ground cover of annual plants in April across 3 important vegetation types for mountain sheep, San Bernardino Co., California, 1990-92. Note the effects of the drought.

differences were apparent in 1991 ($\underline{X}^2$ = 12.90, 2 df, $\underline{P}$ = 0.002) and 1992 ($\underline{X}^2$ = 29.10, 2 df, $\underline{P}$ < 0.001).

Horizontal cover may affect visibility and be important in explaining why male and female sheep use habitats differently. Within vegetation types, horizontal cover was least from 1 - 2 m in height, and greatest < 1 m above the ground (Fig. 8). A Friedman 2-way test indicated significant differences among the 6 vegetation types ($\underline{X}_r^2$ = 16.14, 5 df, $\underline{P}$ < 0.01). I noted a positive correlation between percent horizontal cover and the number of times geomorphic features (e.g. rocks or slope) contributed to that measure for CBS ($\underline{r}_S$ = 0.38, $\underline{P}$ < 0.01), YES ($\underline{r}_S$ = 0.34, $\underline{P}$ < 0.01), TZ ($\underline{r}_S$ = 0.25, $\underline{P}$ < 0.01), RS ($\underline{r}_S$ = 0.79, $\underline{P}$ < 0.001), and Dune ($\underline{r}_S$ = 0.25, $\underline{P}$ < 0.001) vegetation, but not for Wash vegetation ($\underline{r}_S$ = 0.00, $\underline{P}$ = 1.00). For all vegetation types, ground cover was significantly correlated with cover < 1 m above the ground ($\underline{r}_S$ = 0.89, $\underline{P}$ < 0.03) but not for > 1 m in height ($\underline{r}_S$ = 0.37, $\underline{P}$ > 0.25).

Habitat Use

Telemetered males and females used vegetation types differently between segregation and aggregation ($\underline{G}$ = 175.21, 16 df, $\underline{P}$ < 0.001). Females used RS more and CBS less often than did males; use of Dune, Wash, TZ, and YES was approximately equal for males and females (Fig. 10). I noted no difference in the occurrence of females in

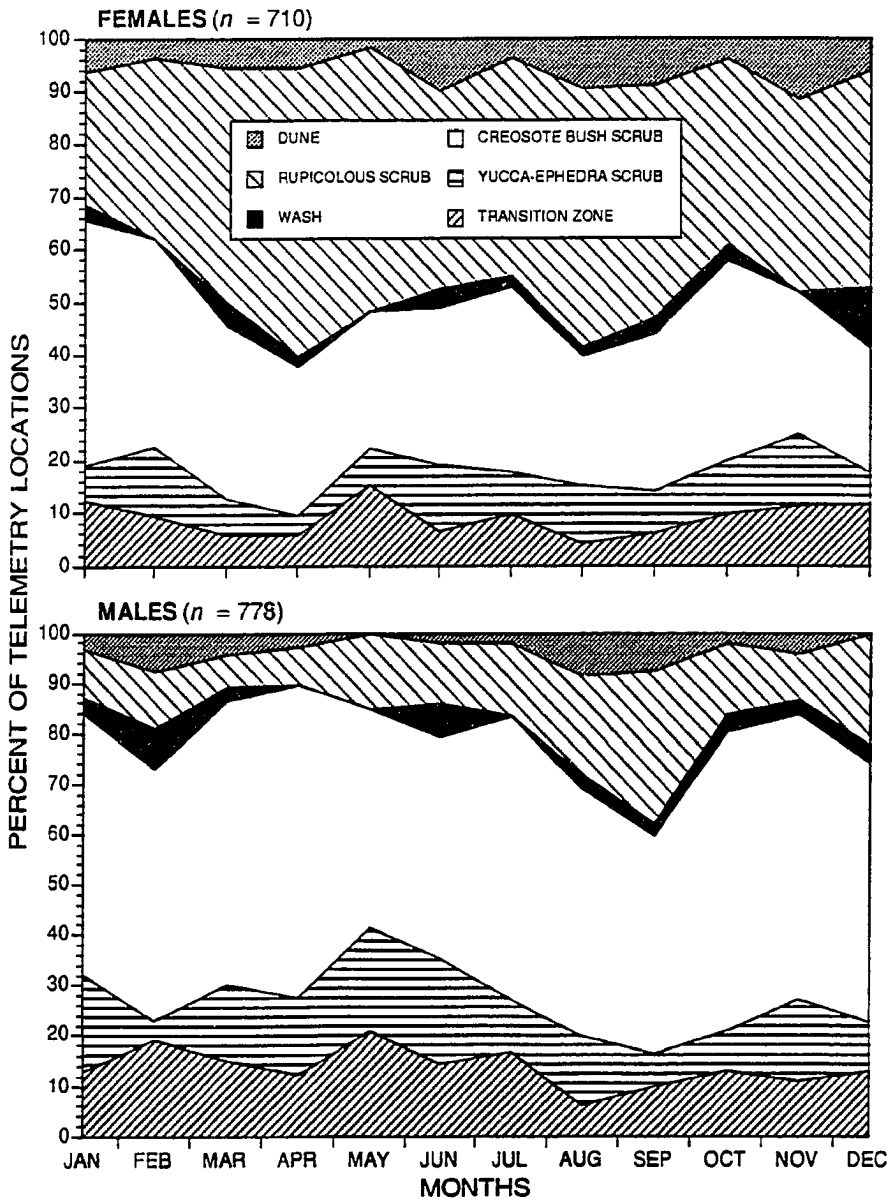

Fig. 10. Percent of telemetry locations for male and female mountain sheep in various vegetative types, San Bernardino Co., California, 1986-90. Note the use of rupicolous scrub by females and use of creosote bush scrub by males.

vegetation types between segregation and aggregation (G = 3.88, 5 df, P = 0.57), but differential occurrence of males among vegetation types was evident (G = 13.80, 5 df; P = 0.02).

To test for differences in physical characteristics of habitat associated with males and females, I examined a suite of variables, including distance to water, elevation, slope, ruggedness, E-W aspect, N-S aspect, and openness. Data from aerial telemetry and those obtained during helicopter observations were examined separately.

For females, a 1-way MANOVA indicated no significant overall difference in the physical characteristics of habitats used between sexual segregation and aggregation (F = 1.39; 7, 702 df; P = 0.21). Females used similar habitats throughout the year (Table 3).

When males were considered separately, a 1-way MANOVA indicated a significant overall difference in habitats used between sexual segregation and aggregation (F = 6.67; 7, 770 df; $P < 0.001$). Males occurred at lower elevations, on steeper slopes, in more rugged terrain, and in more open habitats during aggregation compared to segregation (Table 3).

A 1-way MANOVA indicated significant overall differences in use of physical habitat characteristics between males and females (F = 35.70; 7, 851 df; $P < 0.001$)

during segregation. Females occurred closer to water, at lower elevations, on steeper slopes, in more rugged terrain, and in more open habitats than did males (Table 3). Elevation probably was significant in this model because the study area increased in elevation from west to east, and males moved eastward during segregation. Consequently, males occurred at higher elevations largely independent of other habitat characteristics.

Similarly, when habitat variables were examined during aggregation, a 1-way MANOVA indicated significant overall differences in habitat characteristics between the sexes (F = 7.86; 7, 621 df; $P < 0.001$). Females again occurred closer to water, on steeper slopes, in more rugged terrain, and in more open habitats, but no difference existed in the mean elevation at which females and males occurred (Table 3).

Helicopter surveys showed that female groups without lambs ($\bar{X}$ = 2,145 m, SD = 1,615 m, n = 64) and female groups with lambs ($\bar{X}$ = 2,234 m, SD = 1,764 m, n = 68) occurred at similar distances to free water during aggregation. Likewise, there was little difference in distance to water for these same groups during sexual segregation (without lambs, $\bar{X}$ = 2,553 m, SD = 1,788 m, n = 165; with lambs, $\bar{X}$ = 2,533 m, SD = 1,967 m, n = 133). ANOVA (1, 426 df) demonstrated no effect of the presence of a lamb on distance

to water (F = 0.64, P = 0.42), a marginally nonsignificant effect of period (segregation and aggregation) (F = 3.19, P = 0.08), and no lamb by period interaction (F = 0.27, P = 0.60). When steepness of slope and ruggedness of terrain were held as covariates (ANCOVA, 3, 424 df), there was a highly significant effect of period (F = 6.83, P = 0.01), but no effect of the presence of a lamb (F = 0.83, P = 0.36) or an interaction between these variables (F = 0.80, P = 0.37). Thus, when effects of potential escape terrain were held constant, females occurred closer to water during the hot months that composed the period of aggregation (especially Aug and Sep; Fig. 2) and occurred further from water during segregation. This outcome suggests that suitable terrain constrains the use of water by females. There was, however, no effect of whether a female group contained a lamb.

Mature and young males occurred similar distances from free water during both aggregation (Class II, $\bar{X}$ = 2,642 m, SD = 2,362 m; Class III and IV, $\bar{X}$ = 2,500 m, SD = 1,843 m) and segregation (Class II, $\bar{X}$ = 3,332 m, SD = 2,037 m; Class III and IV, $\bar{X}$ = 3,050 m, SD = 1,944 m), even though class II males had substantially lower body mass than class III and IV males (Table 1). Like females, males occurred closer to water during aggregation than segregation (ANOVA, F = 3.78; 1, 405 df; P = 0.05). No difference occurred, however,

between size classes of males (F = 0.01, P = 0.93); there was no period by size class interaction (F = 0.01, P = 0.93).

During segregation, females with lambs were observed on steeper slopes in more open areas than those without lambs; they also inhabited more rugged terrain, but not significantly so (Table 4). Such differences were not observed during aggregation, when lambs were older (ca. 6 mo-of-age). With periods (segregation and aggregation) combined, female groups with lambs occurred in different terrain than females without young (MANOVA, F = 8.36; 6, 860 df, $P < 0.001$); significant differences ($P < 0.05$) occurred for elevation, slope steepness, ruggedness, and openness. Females with young occurred in areas with terrain characteristics that provided greater potential for evading predators.

Mature (class III and IV) males were observed in areas with different terrain characteristics than were groups containing only younger males (class II) during segregation, but not during aggregation (Table 5). With periods combined, mature males used terrain characteristics differently than young ones (MANOVA, F = 2.43; 6, 400 df; P = 0.03); such differences ($P \leq 0.05$) were pronounced, with mature males in less open and less rugged terrain.

Table 4. Characteristics of terrain in which female groups without lambs and female groups with lambs were observed during helicopter surveys, San Bernardino Co., California, 1981-90.

Terrain Characteristics	Female Groups: Segregation: with lambs (n = 133) $\bar{X}$	SD	P^a	Segregation: without lambs (n = 165) $\bar{X}$	SD	Aggregation: with lambs (n = 68) $\bar{X}$	SD	P^a	Aggregation: without lambs (n = 64) $\bar{X}$	SD
Elevation (m)	910	169	NS	935	161	884	167	NS	865	175
Slope (%)	34	18	*	27	18	28	17	NS	28	15
Ruggedness (index)	27	13	NS	24	13	23	12	NS	26	12
E-W Aspect (SIN°)	0.06	0.70	NS	-0.03	0.73	0.11	0.76	NS	-0.07	0.67
N-S Aspect (COS°)	-0.04	0.72	NS	-0.03	0.68	0.02	0.65	NS	0.05	0.74
Openness (Rank, 1= most open)	2.6	1.1	*	3.0	1.3	2.8	1.1	NS	2.6	1.0

[a] P-values are corrected Bonferroni comparisons within periods of segregation and aggregation; NS = not significant, * = $P \leq 0.05$. No significant differences occurred between segregation and aggregation (MANOVA; $F = 1.71$; 6, 860 df; $P = 0.12$).

Table 5. Characteristics of terrain in which groups of mature males (class III and IV) and groups of only young males (class II) were observed during helicopter surveys, San Bernardino Co., California, 1981-90.

Terrain Characteristics	Male Groups									
	Segregation					Aggregation				
	Class II (n = 23)			Class III & IV (n = 161)		Class II (n = 13)			Class III & IV (n = 107)	
	$\bar{X}$	SD	P[a]	$\bar{X}$	SD	$\bar{X}$	SD	P[a]	$\bar{X}$	SD
Elevation (m)	897	219	*	1,018	186	958	103	NS	968	167
Slope (%)	21	19	*	13	11	23	14	NS	22	16
Ruggedness (index)	21	14	*	13	8	22	16	NS	19	11
E-W aspect (SIN°)	-0.01	0.79	NS	-0.01	0.70	0.33	0.62	NS	0.02	0.69
N-S aspect (COS°)	0.18	0.65	NS	0.06	0.72	0.04	0.76	NS	-0.07	0.69
Openness (rank, 1 = most open)	3.5	1.2	*	4.1	1.0	2.8	1.2	NS	3.4	1.3

[a] P-values are corrected Bonferroni comparisons within periods of segregation and aggregation.

Habitat Selection

Because females used the same range year-round, and no difference occurred in use of vegetation types between segregation and aggregation (see **Habitat Use**; Fig. 10), habitat selection for females was determined on a yearly basis. Females strongly selected (use > availability) RS and avoided (use < availability) other vegetation types, except YES, which was used in proportion to its availability ($\underline{X}^2$ = 3,698.5, 5 df, $\underline{P}$ < 0.001; Fig. 11).

During sexual segregation, significant differences existed in the selection of vegetation types by mature male mountain sheep ($\underline{X}^2$ = 242.8, 5 df, $\underline{P}$ < 0.001) and this pattern was nearly identical during aggregation ($\underline{X}^2$ = 389.4; 5 df; $\underline{P}$ < 0.001). Males selected CBS and RS, and used YES in proportion to its availability; males avoided other vegetation types during both segregation and aggregation (Fig. 11).

Log-likelihood models indicated that mature males selected vegetation types differently than did females during segregation ($\underline{X}^2$ = 109.7, 5 df, $\underline{P}$ < 0.001) and aggregation ($\underline{X}^2$ = 32.3, 5 df, $\underline{P}$ < 0.001). Differential selection between the sexes occurred for CBS; females selected RS more strongly than did males (Fig. 11).

Year-round differences existed in the selection of slope categories by females ($\underline{X}^2$ = 2,313.7, 8 df, $\underline{P}$ < 0.001).

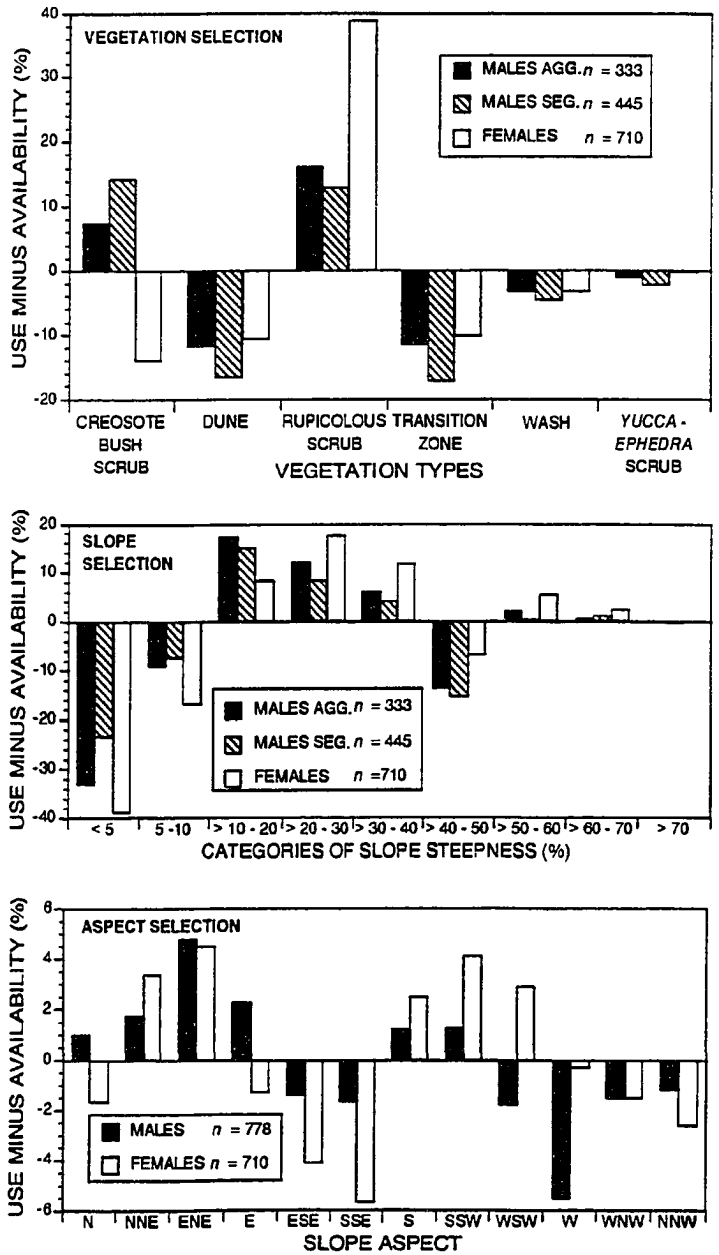

Fig. 11. Selection (% use - % available) of vegetation types, slope categories, and aspect categories by male and female mountain sheep, San Bernardino Co., California, 1986-90.

Generally, females avoided slopes from 0-10%, as well as those > 40-50%; they selected slopes > 10 and < 41%, as well as slopes > 70% (Fig. 11).

During segregation, significant differences existed in the way that males selected slope categories ($\underline{X}^2$ = 348.8, 8 df, $\underline{P}$ < 0.001). Males avoided slopes from 0-10%, as well as slopes from 41-50% and > 70%; males selected slopes from 11-40% (Fig. 11). During aggregation, significant differences again existed in the way that males selected categories of slope steepness ($\underline{X}^2$ = 461.7, 8 df, $\underline{P}$ < 0.001). During aggregation, males used the steepest slope category (> 70%) in proportion to its availability, whereas they avoided this same slope category during segregation (Fig. 11).

Log-likelihood models indicated significant differences in the selection of slope steepness by males and females during segregation ($\underline{X}^2$ = 121.2, 5 df, $\underline{P}$ < 0.001) and aggregation ($\underline{X}^2$ = 35.6, 5 df, $\underline{P}$ < 0.001). These tests required that the 4 categories reflecting extremely steep slopes (> 40%) be combined. In general, females avoided more level terrain and selected steeper slopes more strongly than did males, especially during segregation (Fig. 11).

Because there was no difference in the way that males and females used slope aspects between segregation or aggregation (Table 5), I examined selection of this variable on an annual basis. Significant differences existed in the

manner in which female mountain sheep selected slope aspects (χ^2 = 92.2, 11 df, $P < 0.001$). Females selected primarily northeasterly and southwesterly slopes, while avoiding southeasterly and northwesterly aspects (Fig. 11). Similarly, significant differences existed in the way that male mountain sheep selected aspects (χ^2 = 110.9, 11 df, $P < 0.001$). Males selected slopes facing ENE, and avoided west-facing aspects; all others were used in proportion to their availability (Fig. 11).

Log-likelihood models indicated differences between the sexes in the manner in which they selected categories of slope aspect during segregation (χ^2 = 31.3, 11 df, $P = 0.001$) and aggregation (χ^2 = 36.2, 11 df, $P < 0.001$). This pattern was near identical for both periods, with the direction of selection by the sexes differing on N, E, and WSW exposures, and females more strongly avoiding ESE and SSE aspects; males more strongly avoided W-facing slopes (Fig. 11).

Because the availability of water on ranges occupied by males and females could be a factor explaining the distance that the sexes occurred from water, it was necessary to control for that possibility. To do so, I determined the mean difference between the distances that telemetered male (n = 445) and female (n = 414) sheep, and equal numbers of random points, occurred from water. A 1-way ANOVA indicated

that females ($\bar{X}$ = -3,243.7 m, SD = 3,777.3 m) occurred significantly closer to water than did males ($\bar{X}$ = -1,648.0 m, SD = 3,190.9 m), when compared to random points (F = 44.94; 1, 857 df; $P < 0.001$). When the relative availability of water on male and female ranges is taken into account, females still selected areas closer to water than did males during segregation.

Forage Availability and Quality

Both the distribution and diet of sheep may be influenced, in part, by availability of forage within vegetation types. Mature males moved to ranges largely disjunct from those of females during segregation (Fig. 7). Likewise, males and females used vegetation types differently during this period (Fig. 10), and these types varied markedly in size (Fig. 3). Further, forage availability (% cover) also differed among vegetation types (Fig. 8). Consequently, forage available to sheep is a function of both vegetative cover within a habitat and the relative size of that vegetation type. Mature males occurred predominantly in CBS and YES, and females in RS during segregation (Fig. 10). When both the cover of vegetation and size of vegetation type were considered, males clearly used areas with more forage than did females (Fig. 12).

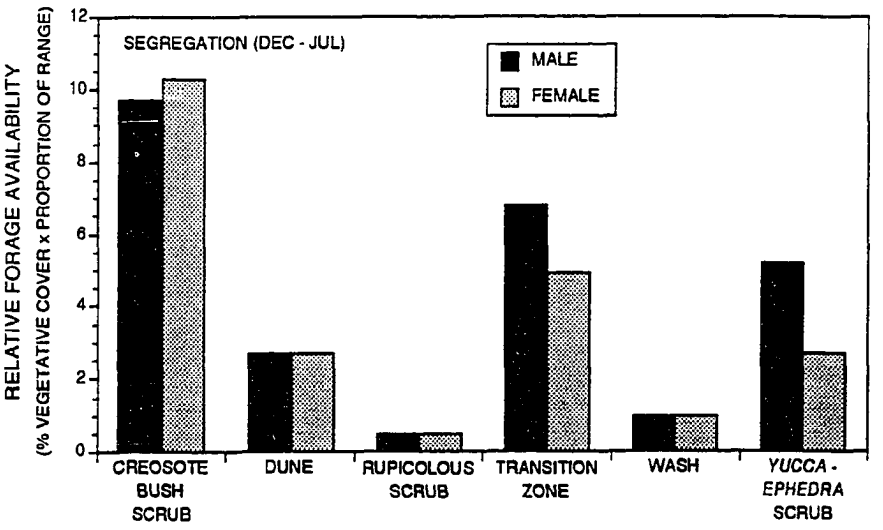

Fig. 12. Availability of potential forage in 6 vegetation types used by mountain sheep during sexual segregation, San Bernardino Co., California, 1990.

To examine the potential role of forage in explaining sexual segregation, I tested for overall differences in food quality (moisture content, CP, and IVDMD) of 20 plant species eaten by mountain sheep using data from Bleich et al. (1992b). One-way MANOVA's indicated significant monthly effects on quality for grasses (F = 4.23; 33, 266 df; P < 0.001), perennial forbs (F = 2.50; 33, 26 df; P = 0.009), and shrubs (F = 5.02; 33, 659 df; P < 0.001) (Fig. 13). Inadequate samples of succulents precluded their use in this analysis, and data for perennial and deciduous shrubs were pooled. On an annual basis, perennial forbs had the highest levels of CP ($\bar{X}$ = 14.2%, SD = 3.4%), IVDMD ($\bar{X}$ = 52.5%, SD = 7.2%), and moisture content ($\bar{X}$ = 55.8%, SD = 11.5%), and grasses had the lowest levels of CP ($\bar{X}$ = 6.9%, SD = 2.8%), IVDMD ($\bar{X}$ = 40.3%, SD = 6.9%), and moisture content ($\bar{X}$ = 32.5%, SD = 16.9%). Perennial shrubs were intermediate in CP ($\bar{X}$ = 10.3%, SD = 4.3%), IVDMD ($\bar{X}$ = 43.4%, SD = 16.0%), and moisture content ($\bar{X}$ = 44.4%, SD = 14.3%). There were clear increases in the overall quality of these forage classes from February to May (Fig. 13).

When an overall model compared quality of forage classes during segregation and aggregation on ranges inhabited primarily by mature males or females, and their interaction term (period of segregation-aggregation by sex), the outcome was highly significant (F = 6.46; 3, 357 df; P <

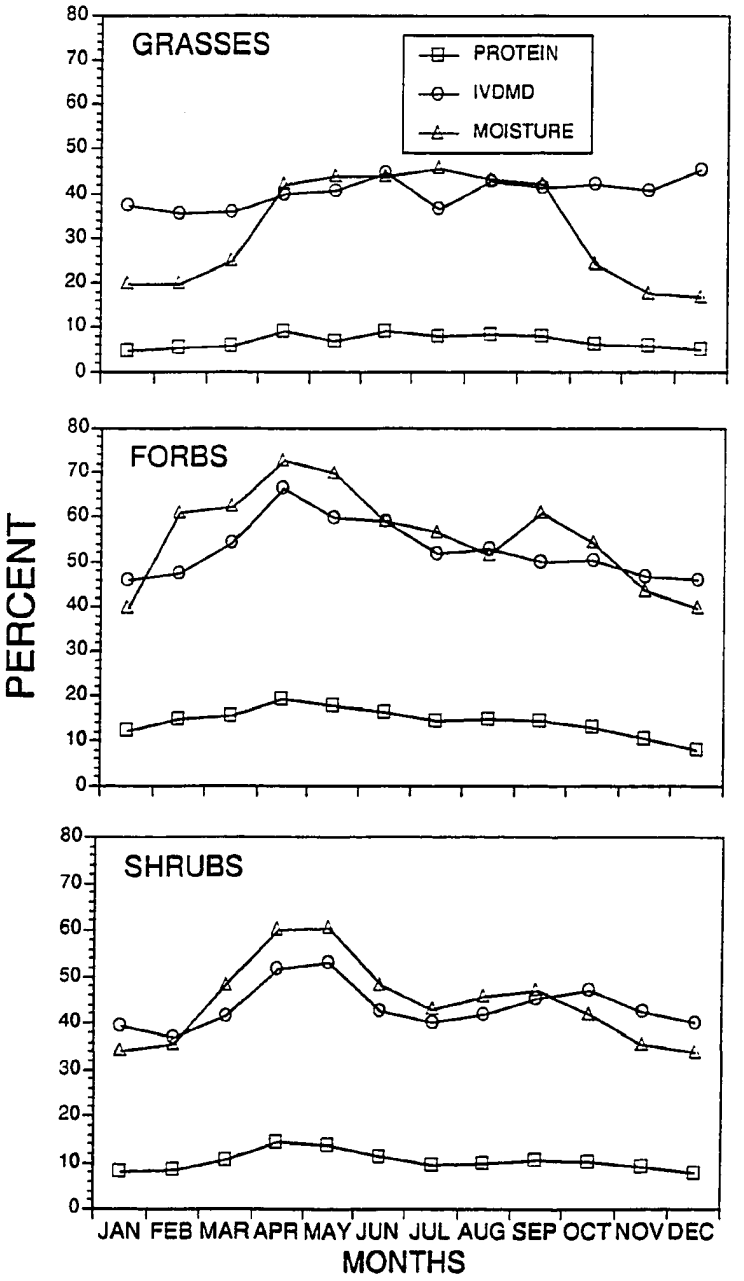

Fig. 13. Quality of forage classes eaten by mountain sheep in San Bernardino Co., California, 1990-91. Data were adapted from Bleich et al. (1992b).

0.001). Examination of univariate F-statistics, however, clearly indicated this model was primarily influenced by moisture content (F = 9.04, P = 0.03) compared to CP (F = 0.15, P = 0.70) or IVDMD (F = 0.14, P = 0.71). Increased moisture content on areas inhabited primarily by females probably was not a good measure of overall forage quality because similar increases in CP and IVDMD were not evident.

Diet

To compare the diets of males and females, I examined the percent composition of annual plants, perennial grasses, perennial forbs, shrubs, and succulents in the feces of mountain sheep (Fig. 14). There was both intra- and interannual variation in the way that male and female sheep consumed these forage classes (Table 6). During the period of sexual segregation between July 1987 and June 1988, male sheep fed more extensively on annuals, shrubs, and succulents than did females, while females ate more grasses and forbs than did males. During aggregation, females fed more extensively on perennial forbs, shrubs and succulents than did males, while males ate more annuals and perennial grasses.

During segregation from July of 1988 to June 1989 (Fig. 14, Table 6), males consumed more shrubs and succulents than did females, whereas females consumed more annuals, perennial forbs, and perennial grasses. During aggregation,

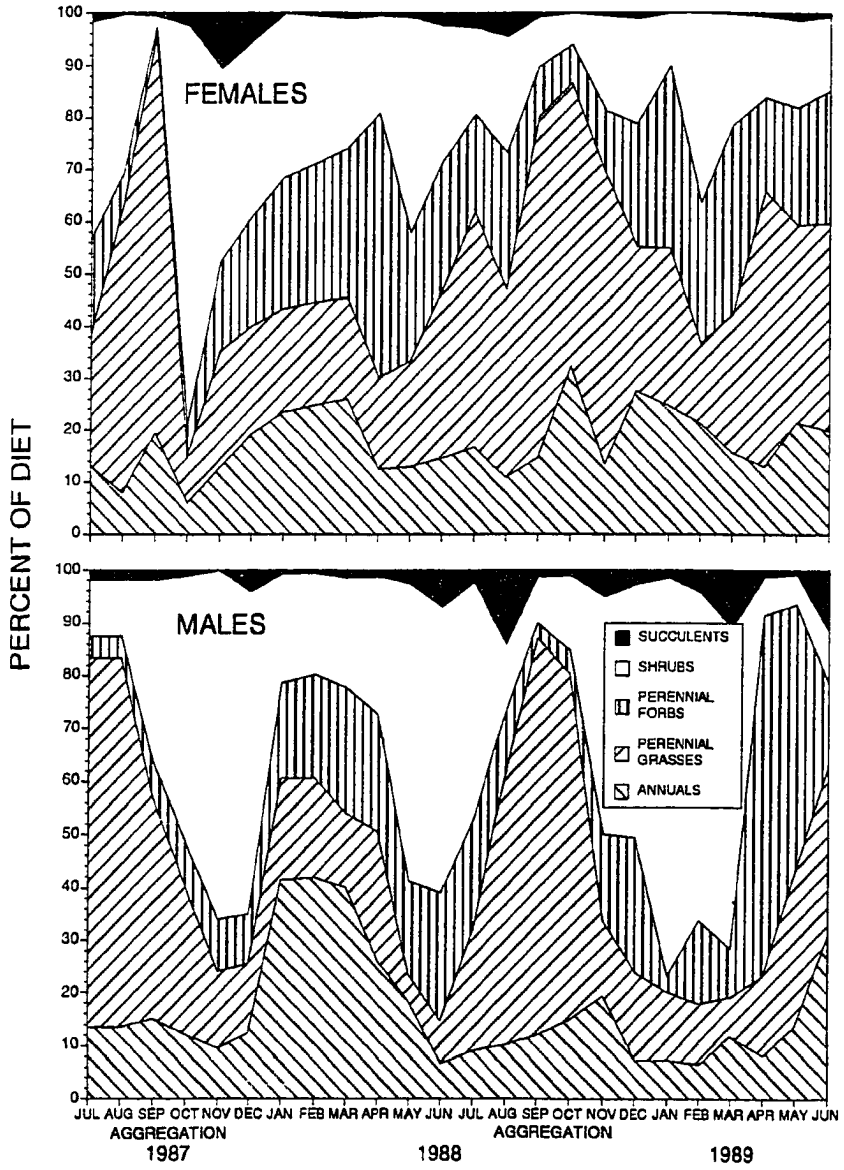

Fig. 14. Percent of various forages in the diets of female and male mountain sheep, indexed from microhistological analysis of their feces, San Bernardino Co., California, 1987-89. Periods of sexual aggregation (August - November) are indicated. Missing values (females, December 1987, February 1988; males, July, October 1987) are calculated from adjacent months.

Table 6. Percent of forage classes in the diets of male and female mountain sheep, San Bernardino Co., California, 1987-89.

Season	Sex	Percent of Forage Class[a]				
		Annual	Per. Grass	Per. Forb	Shrub	Succu-lent
1987-88						
Seg.	F	17.1	22.5*	28.6	20.8	1.0*
		11.0	11.5	17.0	20.2	1.6
	M	24.3	14.3*	19.6	39.0	2.8*
		15.5	9.2	8.7	20.7	4.1
Agg.	F	9.6	31.0*	8.0	47.9	3.5
		7.8	25.9	8.0	28.4	6.6
	M	13.8	50.3*	6.1	28.1	1.8
		6.5	20.9	3.9	20.3	1.8
1988-89						
Seg.	F	19.4*	35.4*	25.5	18.3*	0.8*
		9.2	14.5	10.2	11.6	1.3
	M	11.6*	16.7*	24.6	42.0*	5.3*
		10.9	9.9	25.2	32.3	14.0
Agg.	F	16.8	54.1	13.7	14.0	1.4*
		10.2	22.0	14.5	12.7	4.3
	M	13.5	52.9	8.8	18.5	6.3*
		6.5	25.9	8.3	19.9	10.0

[a] Data presented for each season, period and sex are means (first row) and standard deviations (second row). Statistical comparisons are between males and females within seasons and periods. MANOVAs, for year ($F = 6.17$; 5, 118 df; $P < 0.001$), month ($F = 10.99$; 35, 582 df; $P < 0.001$), and sex ($F = 12.04$; 5, 118 df; $P < 0.001$) were significant.

* $P \leq 0.05$

males fed more extensively on shrubs and succulents than did females, and females ate more annuals, perennial grasses, and perennial forbs (Fig. 14).

Diet Quality

As an index to diet quality, I compared FCP values of males and females (Fig. 15). There was both intra- and interannual variation in FCP between the sexes (Table 7). FCP of males was higher than that of females during segregation in 1987-88 and 1988-89, but did not differ from that of females in 1989-90. In 1988-89, females had significantly higher FCP during aggregation, but no differences existed between males and females during aggregation in 1987-88 or 1989-90.

That FCP indexed diet quality for mountain sheep is indicated by the correspondence between protein levels in the feces (Fig. 15) and measures of forage quality (Fig. 13); both these indices were elevated during spring. Males did consume more shrubs than females (Table 6), and tannins possibly increased levels of FCP at that time. This is unlikely, however, because there was no relationship between the percent of shrubs in the diet and FCP for either males ($\underline{r}^2 < 0.01$; 1, 88 df; $\underline{P} = 0.44$) or females ($\underline{r}^2 < 0.001$; 1, 120 df; $\underline{P} = 0.91$).

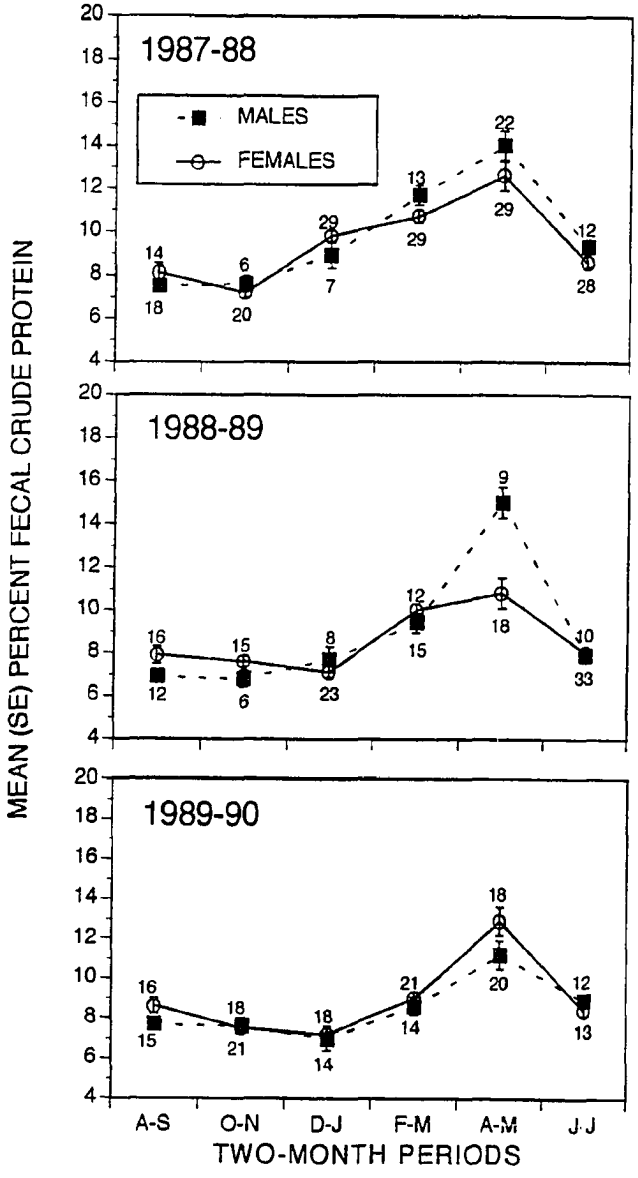

Fig. 15. Fecal crude protein of male and female mountain sheep, by 2-month periods over 3 years, San Bernardino Co., California, 1987-90. The third year (1989-90) reflects drought conditions.

Table 7. Fecal crude protein levels of male and female mountain sheep, San Bernardino Co., California, 1987-90.

Year	Period	Fecal Crude Protein						P[a]
		Female			Male			
		$\bar{X}$	SD	(n)	$\bar{X}$	SD	(n)	
1987-88	Seg	10.45	2.76	(115)	11.76	3.18	(54)	0.007
	Agg	7.53	1.35	(34)	7.51	0.78	(24)	0.950
1988-89	Seg	8.64	2.14	(86)	9.92	3.39	(42)	0.010
	Agg	7.74	1.05	(31)	6.90	0.80	(18)	0.005
1989-90	Seg	9.40	2.49	(70)	9.17	2.00	(60)	0.565
	Agg	8.01	1.03	(34)	7.63	0.80	(36)	0.080

[a] P-values are from Tukey post-hoc comparisons of mean fecal crude protein within years and periods

Abundance of Predators

To examine the relative abundance of potential predators in habitats used by male and female mountain sheep, I calculated three indices of predator abundance. From June 1987 to August 1990, a total of 740 km of transects (n = 93) was hiked (Fig. 16). Sampling occurred in 2 areas occupied predominantly by mature male sheep during sexual segregation (East Hills and Kelso Mountains), and in 2 areas inhabited mostly by females (Old Dad Mountain and Cowhole Mountain). When feces from all predators were combined within each area, there were significant differences in the densities among these 4 sampling areas (F = 26.15; 3, 91 df; $P < 0.001$); predator feces occurred at higher densities in those areas used predominantly by males (Fig. 16). No scats of mountain lions were located.

Predators recorded by time-lapse photography (animals/10,000 frames of film) at water sources were more frequent on ranges of mature males than those used by females (Z = 6.18; $P < 0.001$). This pattern was especially pronounced for coyotes (Fig. 16). Again, no mountain lions were photographed.

A 1-way ranked ANOVA failed to detect significant differences in rates of aerial observation for all predators (F = 0.39; 4, 71 df; P = 0.81). Nonetheless, bobcats and coyotes were observed more often in areas used predominantly

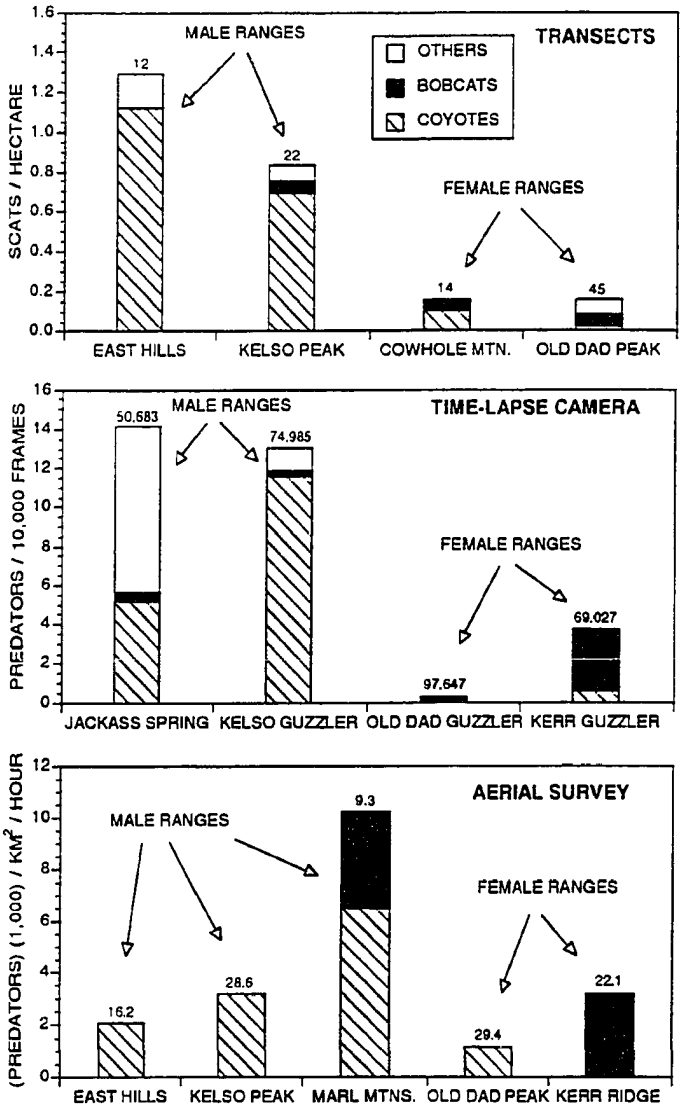

Fig. 16. Relative abundance of predators on ranges occupied primarily by mature male or female mountain sheep, San Bernardino Co., California, 1987-90. Scats were counted from June 1987 to August 1990, cameras operated from July 1988 to June 1990, and aerial surveys were conducted from March 1987 to December 1990. Sample sizes are presented above bars; for scats n = transects, for cameras n = photographic frames, and for aerial surveys n = hours.

by males. This pattern was consistent with scat transects and photography (Fig. 16). No mountain lions were observed during aerial surveys.

Causes of Mortality and Evidence of Sheep in Carnivore Diets

At least 4 male mountain sheep were killed by mountain lions, and 1 male drowned in a steep-sided tenaja (Appendix B). Three other males and 1 female died of unconfirmed causes. These carcasses were located in relatively flat terrain, and had been scavenged by coyotes.

To determine the importance of ungulates in the diet of carnivores, I examined 120 predator scats. Remains (hair) of mountain sheep were detected in 3.1% of 97 coyote scats, 0% of 12 bobcat scats, and 0% of 11 fox scats. No other evidence of ungulates (e.g. bones, hooves) was present in the feces of predators. None of the scats examined contained remains of other ungulates.

DISCUSSION

Sexual Dimorphism and Hypotheses Explaining Sexual Segregation

Sexual dimorphism in body size and secondary sexual characteristics are pronounced in North American wild sheep (Shackleton 1985, Bowyer and Leslie 1992, for reviews). Indeed, desert-dwelling mountain sheep exhibited a marked dimorphism in body mass that increased with age (Table 2). Likewise, as Geist (1971) documented, larger, older males typically possessed bigger horns.

A difference in body mass may be a crucial factor in understanding why the sexes segregate, because it affects social behavior (Geist 1971), susceptibility to predation, and results in strong allometric differences (Table 1). Most hypotheses forwarded to explain sexual segregation invoke morphological differences between the sexes (Main and Coblentz 1990, Miquelle et al. 1992).

Miquelle et al. (1992) cautioned that there may be no single, universal explanation for sexual segregation in ungulates; there are some hypotheses, however, that may be removed from serious consideration. Indeed, the weight of evidence from this, and other studies, suggests that some hypotheses are sufficiently incompatible with observed

patterns of sexual segregation that they can be rejected, or at least be considered highly unlikely, for most ungulates. Consequently, I do not believe that additional effort and tests of these notions are likely to yield fruitful results.

The first of these hypotheses, that males may be less tolerant of areas heavily contaminated by feces because they are more likely to suffer from increased parasite loads than are females (Clutton-Brock et al. 1987), seems unlikely (Miquelle et al. 1992). Indeed, Clutton-Brock et al. (1987) refuted this hypothesis for red deer. Although mountain sheep in some areas may be severely affected by a nematode parasite in which first-stage larve are passed in the feces (Shackleton 1985), this lungworm (Protostrongylus) does not occur on most desert ranges (Clark et al. 1985). Moreover, other fecal-borne diseases are not thought to be important mortality factors for desert sheep, and males are not known to be more susceptible than females (Clark et al. 1985). Consequently, males avoiding fecal-contaminated areas is not a viable hypothesis explaining sexual segregation for desert-dwelling mountain sheep. In the absence of any supportive evidence, no further consideration of this hypothesis seems warranted.

A second notion that likely can be laid to rest is that segregation of the sexes results from males avoiding aggressive interactions provoked by the presence of females.

Geist (1971) did observe low-intensity interactions between male sheep outside rut, but whether these would have developed into serious fights in the presence of females is questionable. As Main and Coblentz (1990) aptly noted, rutting behaviors (including aggression) are regulated by hormones that are highly seasonal. If this hypothesis were correct, young males (class I and II), many of which remain with females outside rut (Fig. 5) and are sexually mature (Turner 1976), should continue to engage in fights as well as other rut-related behaviors. I did not observe these intense interactions in my study population.

Verme (1988) speculated that male cervids might segregate because they require more open areas to prevent damage to growing antlers. Obviously, this hypothesis is applicable only to cervids; bovids do not cast their horns (Main and Coblentz 1990). Mule deer living in exceptionally open habitats year-round still exhibited sexual segregation (Scarbrough and Krausman 1988). Moreover, male mule deer inhabiting vegetation types varying from dense brush to open meadows did not use habitats differently during periods of segregation and aggregation (Bowyer 1984, 1986a). These outcomes make this hypothesis an extraordinarily unlikely explanation for sexual segregation for ungulates in general, and raise questions about its validity for cervids. I suggest that this hypothesis be set aside until additional

evidence is obtained that cervids behave in the predicted manner, and that this behavior is related to injury of antlers.

McCullough (1979) and Verme (1988) suggested that males might segregate to more open areas where they could maintain visual contact and thereby adequately evaluate the dominance status of other males. This hypothesis infers that ungulates inhabiting open lands should not segregate (i.e., there is no reason for males to move away from females). Contrary evidence is available from a number of cervids (Main and Coblentz 1990). Additionally, this hypothesis will not explain why about one-half of class II males in my study remained with females. Moreover, ungulates posses other means of recognizing conspecifics and their status besides vision (e.g. olfaction--Coblentz 1976, Bowyer and Kitchen 1987). The size of horn-like organs is often an indication of the hierarchical status of a male (Geist 1971, Hirth 1977, Kucera 1978, Bowyer 1986b, and many others). This assessment of dominance, however, does not require especially open areas. Also, this hypothesis does not explain why males should remain segregated for such an extended period. Indeed, sparring (ritualized fighting in which males assess dominance) is most often focused around rut when the sexes are at least partially aggregated (Geist 1971, Bowyer 1986b) Although males may have opportunities

to assess the dominance of potential rivals during segregation, there is no compelling evidence that this leads to segregation--this hypothesis should be rejected.

Geist and Bromley (1978) proposed two thought-provoking ideas about why the sexes should segregate following rut. First, male cervids may spatially separate from females following mating, but then return after antler casting because mimicry of females allows them to rejoin such groups without being conspicuous to predators. As with other hypotheses related to the casting of antlers (or horn sheaths), this idea only may be applied to cervids (and perhaps antilocaprids), and may not be invoked as a general explanation for sexual segregation in ungulates. Moreover, this hypothesis will not suffice to explain segregation beyond the time of antler casting or where segregation is more pronounced during spring when antler regrowth is obvious (Bowyer 1984, McCullough et al. 1989). Miquelle et al. (1992) concluded that the presence of antlers did not appear to be an important factor influencing the distribution of the sexes for moose following rut. Too much contrary evidence exists to make this a viable hypothesis, and it should be set aside unless strong corroborative data are forthcoming.

Second, Geist and Bromley (1978) suggested that males that retain their horn-like organs through winter should

segregate from females to avoid being conspicuous because of their increased vulnerability to predation, a result of strenuous rutting activities. This hypothesis may be applicable to both cervids and bovids, because both horns and antlers would be conspicuous for at least some period following rut. Indeed, male ungulates often predominate in the kills of predators (McCullough 1979). This hypothesis, however, poorly explains the timing of segregation for some cervids. For instance, mule deer remain segregated following antler casting and well into the period of antler regrowth (Bowyer 1984). Moreover, this idea would not explain why adult male mountain sheep in this study moved to areas with more predators during segregation, and suffered higher mortality. Horns and antlers may offer a cue to predators in identifying vulnerable rut-exhausted males, but this hypothesis will not explain the observed patterns of sexual segregation among most ungulates.

Males might seek habitats with cover that helps minimize energy losses following rut (Staines 1976, Watson and Staines 1978). Clutton-Brock et al. (1987) and Miquelle et al. (1992), however, observed contradictory behavior in red deer and moose, respectively. Obviously, a harsh winter climate is an improbable explanation for segregation for mountain sheep in desert environments. Indeed, the period of segregation in this study encompassed a wide variety of

climatic conditions (Fig. 2), suggesting this was not the cause of segregation in these ungulates. Additionally, sheep aggregated at a time in which the climate was most thermally stressful (Figs. 2, 4). Climate may play an important role in habitat selection by ungulates, but evidence that it causes sexual segregation is not compelling.

An important consideration that sometimes has been overlooked, is that hypotheses forwarded to explain sexual segregation must account for the spatial separation of the sexes, and not merely changes in group composition and association of the sexes (Bowyer 1984). I believe that 4 remaining hypotheses (Table 1) meet this criterion, and have some promise as a general explanation for sexual segregation among ungulates.

Predictions of Hypotheses Versus Empirical Observations

Hypothesis 1: Sexual segregation occurs because mature males avoid areas occupied by females to decrease competition with their offspring and potential mates. -- Numerous authors have ruled out this idea because it was thought to require group selection (McCullough 1979, Morgantini and Hudson 1981, Bowyer 1984, Verme 1988, Main and Coblentz 1990, Miquelle et al. 1992). Nonetheless, there has been no empirically based test of this idea, proposed by Geist and Petocz (1977), even though it

potentially explains the observed pattern of segregation for the sexes of some ungulates.

Contrary to the expectations of this hypothesis, diet quality of mature male sheep (as indexed by fecal crude protein, FCP) was better than that of females during sexual segregation for 2 of 3 study years (Fig. 15). That FCP reflected observed changes in the quality of forage species (Fig. 13) and was not related to the percent of shrubs in the diet, strongly suggests this index to diet quality was not biased by plant secondary compounds. Indeed, FCP repeatedly has been used as a cue to changing quality of diets in wild sheep (Hebert 1973, Wehausen 1980, Seip and Bunnell 1985, Perry et al. 1987, Festa-Blanchet 1988a, Rachlow and Bowyer in press). Similarly, FCP was not likely affected by differential water requirements of males and females, because urea levels in blood plasma were relatively unaffected by 3 days of dehydration in desert-adapted mountain sheep (Turner 1973:70).

Cover of potential forage, likewise, was greater in vegetation types inhabited primarily by mature males (CBS, YES, TZ) compared to vegetation (RS) used mostly by females (Fig. 8). This trend was especially evident for the cover of annual plants in nondrought years (Fig. 9). Moreover, when the area of available vegetation types is considered, the pattern is even more evident because the RS type used by

females composed a relatively small part of sheep range (Figs. 3, 12). This relationship is further exacerbated by population density. Although males occurred at a higher overall density, 42% of females occurred in RS, a vegetation type which composed only 3% of the study area. This concentration of sheep further reduced the availability of forage per individual female. None of these observed outcomes is consistent with males moving to lower-quality areas to benefit offspring and mates.

Although large males (class III and IV) spatially segregated from females, so did many class II males (Fig. 5). Class II males seldom copulate with females (Geist 1971, Hogg 1987) because they are subordinate to these large males during rut. Based on the occurrence of mixed groups (Fig. 4) and a prolonged lambing period, rut for these desert-dwelling sheep occurs over an extended period (at least 4 mo). Consequently, it is unlikely that class II males were able to obtain copulations even from females that underwent a second estrus, because of the association of mature males with females through this extended period. The period of lambing (and hence rut) may be much shorter for populations of sheep at more northern latitudes (Bunnell 1982, Rachlow and Bowyer 1991).

Young male mountain sheep may associate with females and lambs until they are no longer subordinate to adult

females (Geist 1971). Because young males are intermediate in body size between mature males and females (Table 2), and possess horns similar in morphology to females (Geist 1971), they may be able to continue to interact socially with adult females. That some young males remain with female groups, while others of the same relative age join male bands, may be a function of relative body size and horn development (Nievergelt 1967). Indeed, because of the protracted lambing season typical of desert-dwelling mountain sheep (Welles and Welles 1961, Bunnell 1982), some young males may be markedly larger and socially more mature than others from the same lamb cohort. Such differences in age may explain the propensity of some young males to remain with females, while others do not. Whatever the reason underlying this phenomenon, the observation that some class II males segregate from the females is inconsistent with the predictions of Geist and Petocz (1977). Moreover, if class II males that did not mate segregated from females to benefit the offspring of unrelated, large males, then group selection must be invoked (McCullough 1979). The onerous conditions necessary for this to occur would seldom, if ever, be met in ungulates (Williams 1966). Consequently, I reject this hypothesis.

Hypothesis 2: Spatial separation of the sexes occurs because mature males, owing to their larger body size and

strength, are less susceptible to predators than smaller-bodied females, and particularly young, and thereby are able to occupy better areas. -- As previously discussed, male mountain sheep obtained a higher-quality diet and occurred on better ranges than did females during sexual segregation (see Hypothesis 1), which is consistent with the predictions of this hypothesis. Likewise, females selected steeper, more open habitats than did males. Presumably, such areas facilitate evasion of predators by smaller-bodied females. This contention is supported by females with lambs occurring in steeper, more rugged terrain than females without young (Table 4). Moreover, predators were far less common on areas inhabited by females than males (Fig. 16), and males predominated in kills made by predators during this study (Appendix B). All of these results strongly support the hypothesis of Geist (1982) that risk of predation plays a major role in sexual segregation.

Increased risks of predation to males could be a function of their using areas with higher nutritional quality or greater abundance of forage and less-rugged terrain (Berger 1991, and this study), but with higher densities of predators. Such behavior may be analogous to risks taken by crop-raiding male Asian elephants (Elaphas maximus; Sukumar and Gadgil 1988). Likewise, male tule elk (C. e. nannodes) foraged in better habitats with a higher

likelihood of predation by mountain lions, than those habitats used by females (Berbach 1991). Indeed, Main and Coblentz (1990) argued that males and females select areas according to different criteria, with females selecting those most suitable for successfully rearing offspring, and males selecting areas where they can maximize body condition.

Some studies of sexual segregation, however, have reported that females obtained a higher-quality diet and occurred on better areas than did males (Watson and Staines 1978, Staines et al. 1982, Beier 1987, Clutton-Brock et al. 1987, Illius and Gordon 1987), and Weckerly and Nelson (1990) concluded that both males and females obtained diets high in essential nutrients. Moreover, measuring just range quality could be misleading, because variation in population density of ungulates on areas occupied by males and females may affect per capita consumption of forage. For instance, Bowyer (1984) reported that female mule deer were segregated onto areas with a greater abundance of preferred forage than ranges inhabited by males. Nonetheless, when the higher density of females was considered, no significant difference in forage availability per individual was noted. Several studies, however, have corrected for differential densities of the sexes, and still concluded females obtained more,

higher-quality forage during segregation than did males (e.g., Watson and Staines 1978, Clutton-Brock et al. 1987).

Perhaps females in some environments can maximize intake of high-quality forage and simultaneously minimize risk of predation. If this hypothesis is correct, then how forage and risk of predation are arrayed in the environment would have a profound effect upon the pattern of sexual segregation and quality of forage obtained by males and females. This idea, however, does not explain why males would segregate from females under these conditions. Such an outcome probably would require invoking Hypothesis 4 to explain segregation under these circumstances.

The behavior of mountain sheep undoubtedly has been influenced by predation throughout their evolutionary history. Indeed, in the absence of serious competition from other ungulates, natural selection may have resulted in a propensity for North American wild sheep to utilize rocky terrain when faced with dangerous situations (Geist 1971). Mountain sheep appear to evade predation through their exceptional eyesight, climbing ability, and use of open areas adjacent to and within rugged terrain (Wishart 1978).

In a review of the literature, Berger (1991) reported that females and lambs using open terrain were more vulnerable to predation than when on steeper slopes. Despite the extensive use of rugged terrain, particularly by

females, Murie (1944), Hayes and Baer (1986), and Sumanik (1987) described wolves successfully hunting mountain sheep by attacking from above, and forcing sheep to flee from steep cliffs to less precipitous terrain. Sumanik (1987) concluded, however, that in 4 of 6 hunts, proximity to escape terrain was the deciding factor that allowed sheep to evade wolves.

In mountain sheep, a highly dimorphic and polygynous species, natural selection has favored large, powerful males with huge horns (Geist 1971). Adequate forage is an important factor limiting body and horn size in these ungulates (Bunnell 1978, Guthrie 1990). Indeed, the importance of maximizing body condition and size may exceed the increased risk of predation; such risks may be undertaken to enhance reproductive success of males (Kurt 1974, Poole and Moss 1981, Poole 1987, Prins 1989). In females, selection has been for behaviors that reduce the risk of predation on individuals and their offspring, sometimes at the expense of nutrient intake. As long as nutrition is sufficient for ovulation, gestation, and lactation, individual females may maximize their fitness by enhancing the survival of their young. Females do this by occupying areas with lower densities of predators, and that allow greater opportunities to evade predators. Findings from this study are consistent with the hypothesis that

female mountain sheep occupy habitats in which they, and their young are less prone to predation but, simultaneously, sacrifice nutrient quality as a tradeoff for security, as demonstrated experimentally by Berger (1991).

Hypothesis 3: Lactating females with young spatially segregate from males because of greater water requirements. -- Mountain sheep living in desert environments are physiologically specialized in terms of their water metabolism (Turner 1973). These sheep drink about 4% of their body mass in water each day to maintain water balance during extreme temperatures in summer; however, during winter, forage with 1.5-3.0 ml of preformed water/g dry weight may preclude the need for free water (Turner 1973). During segregation, the moisture content of forage on areas occupied by females in this study was higher than for ranges with mostly mature males.

Females occurred significantly closer to sources of free water during sexual segregation than did males, and this difference was maintained even when I controlled for water availability. This difference, however, was even more pronounced during aggregation, ostensibly because temperatures were extremely high for about one-half of aggregation (Fig. 2). Tests of whether females with lambs were closer to sources of free water than females without young showed no significant difference during either

segregation or aggregation. Likewise, there was no difference in distance from water between smaller-bodied class II, and larger class III and IV males during either period.

Bowyer (1984) suggested that sexual segregation in mule deer may result from the constraints imposed by lactation on females, and their resultant need for free water. Moreover, he suggested that allometric differences between males and females would allow males to subsist on vegetation containing less moisture. Although males in my study did occur on ranges with a lower moisture content of forage during segregation, females with lambs did not occur closer to water than those without lambs. Adequate escape cover (steep, rugged terrain) may limit the distribution of female sheep whether or not they have lambs at heel. Indeed, when I controlled for terrain characteristics with ANCOVA, the importance of free water to females was further highlighted.

Whatever the cause of females being closer to water than males, it cannot be invoked to explain sexual segregation in this population--the same general pattern with respect to distance from water occurred during both segregation and aggregation. Consequently, lactational requirements for free water in these desert-adapted sheep can be rejected as an explanation for sexual segregation.

Hypothesis 4: Allometric differences between male and female mountain sheep lead to differential uses of food that result in segregation. -- McCullough (1979), Bowyer (1984), and Beier (1987) proposed that allometric differences (rumen volume:body mass ratio) were a likely cause of sexual segregation in ungulates. In contrast to the expectations of this hypothesis, male mountain sheep obtained higher-quality diets than did females (Fig. 15). Moreover, following nondrought periods, annual plants were more abundant on ranges occupied by male sheep than on ranges occupied by females during sexual segregation (Fig. 9). Indeed, forage availability was generally higher on ranges occupied by males (Fig. 8).

The finding that males obtained better quality diets than did females, is sufficient to reject the hypothesis that allometric differences result in sexual segregation in this population. This hypothesis, however, still may be viable for ungulates where females obtain higher-quality diets (see Hypothesis 2). Moreover, differences in diet composition and quality between the sexes of some ungulates may be present, yet difficult to detect. For instance, Bowyer (1984) reported that the major difference in ranges used by male and female mule deer during segregation was the phenological stage of a preferred forage. Likewise, Beier (1987) noted slight, but significant differences in foods

eaten by the sexes of white-tailed deer during segregation. Even small differences in diet may have a profound effect on the productivity of ruminants (White 1983), and thereby lead to segregation of the sexes. Although I was able to reject this hypothesis for mountain sheep, subtle differences in diet quality and composition may affect segregation in other ungulates.

Clutton-Brock et al. (1987) proposed that segregation of the sexes might be caused by females outcompeting males where forage was of high-quality but of low biomass. Consistent with the hypothesis that females competitively exclude males, is the finding that male sheep moved from areas selected by females during sexual segregation (Fig. 7). Additionally, the percent of shrub cover was greater in CBS, an area selected by males during segregation, but avoided by females (Fig. 11). Moreover, as previously discussed, female mountain sheep occurred at substantially higher densities, at least in habitats they selected, than did males during sexual segregation--again consistent with expectations of this hypothesis.

Conflicting with the predictions of the hypothesis, however, is the finding that (following years of normal rainfall) availability of annual plants was higher in habitats used predominantly by male sheep (Fig. 8), as well as the finding that males obtained better-quality diets than

females during 2 of the 3 years of this study (Fig. 15). Because males had higher-quality diets and occurred on better ranges than did females, the hypothesis that competition was the driving force behind sexual segregation is rejected for this population of mountain sheep. Because of low population density and high availability of forage, Miquelle et al. (1992) concluded that competition was not the primary factor responsible for sexual segregation in moose. Although this hypothesis cannot be entirely ruled out for ungulates in which females occur on higher-quality ranges, the lack of confirmatory evidence for this notion leads me to view it with skepticism. I believe that predation (see Hypothesis 2) and allometric differences offer viable alternatives to competition between the sexes as an explanation for sexual segregation.

CONCLUSIONS

The evolutionary significance of sexual segregation in mountain sheep is, in all probability, best understood as the result of differing life-history strategies of males and females (Main and Coblentz 1990). Indeed, my findings support the hypothesis that females maximize their Darwinian fitness by minimizing risks of predation, albeit potentially by compromising nutrient intake.

Among males, reproductive fitness is strongly influenced by body size and condition (Clutton-Brock et al. 1982, Prins 1989, Guthrie 1990), and the larger body size of mature males may make them less susceptible to predation (Berger 1991), especially by small predators such as coyotes and bobcats. Hence, risks associated with foraging in high-quality habitats, which enhance body condition, may increase the probability of fathering offspring. Miquelle et al. (1992) proposed that sexual dimorphism may lead to differences between the sexes that relate to risk of predation, constraints on foraging, habitat use, and even competition. Nonetheless, their model for sexual segregation requires an heterogeneous environment. In such an environment, the sexes can select resources to meet differential costs and constraints.

I extend their model and suggest that the manner in which forage and predation risk are arrayed in such an heterogeneous environment is an important factor in determining how and why the sexes segregate. During sexual segregation, males and females may be adapted differently for foraging and evading predators in their preferred habitats (Lopez Ornat and Greenberg 1990). Thus, sexual segregation might best be viewed as a compromise between optimal foraging and decreasing predation risk (Skogland 1987).

Main and Coblentz (1990) argued convincingly that the strategy of maximizing body condition, and its resultant increased fitness in males of sexually dimorphic species, appears to be widespread, if not universal. Females of such species appear to concentrate on reducing the risks of predation on themselves and their offspring, albeit at the expense of nutrient intake.

I believe such life-history strategies are best viewed from the perspective of how predation risk, forage abundance, and forage quality are distributed in an heterogeneous environment. I further suggest that this relationship may yet provide a universal hypothesis for understanding sexual dimorphism among ungulates.

MANAGEMENT IMPLICATIONS

Ecological differences between male and female mountain sheep have important implications for conservation. Management of mountain sheep in desert ecosystems has centered on the construction of artificial watering devices (Bleich 1983a, Bleich and Pauli 1990), in the belief that both sexes will benefit. Females occurred significantly closer to water than males during segregation and aggregation, even when I controlled for the availability of water. This observation suggests that water developments may be of greatest value if they are constructed in areas used predominantly by females and their offspring, consistent with the views of Seegmiller and Ohmart (1982).

During sexual segregation, males and females used habitats that were distinctively different. Generally, females used areas that were characterized by steep, open, and rugged terrain with low availabilities of annual and perennial vegetation. In contrast, males used areas that were less steep, less rugged, and with greater availabilities of such vegetation. Indeed, areas used by males during sexual segregation often were associated with flats and rolling hills, which occur between mountain

ranges. The importance of these intermountain areas as movement corridors for mountain sheep previously has been emphasized (Schwartz et al. 1986, Bleich et al. 1990a). During segregation, such areas also provide opportunities for mature males to obtain higher-quality forage than the steep, rugged terrain used primarily by females. Intermountain areas should be recognized for their value as foraging areas for male mountain sheep, as well as for their role in facilitating gene flow.

Grazing by range cattle occurs throughout much of the southwest. Although distributional overlap and resultant competition between range cattle and mountain sheep may not be an important limiting factor in some areas (Dodd and Brady 1986, Dodd 1987, Wehausen 1988), range cattle may alter vegetation, particularly cover of grasses, in habitats used by mountain sheep (Wehausen 1992). Allocations for livestock often are based on the amount of ephemeral vegetation occurring on intermountain ranges, under the assumption that mountain sheep seldom use areas away from steep, rugged slopes. Male mountain sheep, however, make extensive use of intermountain areas that are grazed heavily by range cattle. Moreover, emphemeral plants are important in the diets of male sheep. If grazing by range cattle results in competition with mountain sheep for forage, there may be a reduction in suitable habitat for males.

Ultimately, such an outcome would have implications for the population.

In the eastern Mojave Desert, male mountain sheep may be especially prone to predation by mountain lions. Such predation has had severe consequences for mountain sheep in the Granite Mountains, located approximately 40 km south of the study area (Wehausen 1992). During this study, confirmed losses of sheep to mountain lions was restricted to males; however, should mountain lions colonize Old Dad Mountain, serious consequences may result. Although management options in California currently are limited, the effects of lion predation on mountain sheep in the Mojave Desert should be monitored closely.

Finally, the implications of anthropogenic features further restricting movements of mountain sheep should be considered. Kelbaker Road is a narrow, two-lane black-topped highway that separates the study area. Telemetry data indicate that mountain sheep cross Kelbaker Road on a regular basis; some males at Old Dad Mountain during rut migrate across this highway during sexual segregation. With the increasing human population of California, it is probable that little-traveled roads will become more important as public thoroughfares, and that fencing of these roads will occur. If Kelbaker Road is fenced, an important intermountain corridor (Bleich et al. 1990a) will be

eliminated, with potential landscape-level implications (Schwartz et al. 1986) for mountain sheep inhabiting the eastern Mojave Desert.

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Appendix A. Frequency and cover of vegetation in 6 habitat types.

Table 8. Frequency and cover of plants in Yucca-Ephedra Scrub, San Bernardino Co., California.

Species	Total Freq.	Rel. Freq.	Rel. Cover	SD Cover
Annual Vegetation	2	0.01	1.08	1.94
Acacia greggii	0	0.00	0.08	0.45
Acamptopappus sphaerocephalus	0	0.00	0.12	0.33
Ambrosia dumosa	13	0.12	2.95	3.01
Amphipappus fremontii	0	0.00	0.08	0.34
Arenaria macradenia	0	0.00	0.04	0.28
Aristida adscencionis	0	0.00	0.04	0.28
Bebbia juncea	0	0.00	0.04	0.20
Cassia armata	0	0.00	0.06	0.24
Ceratoides lanata	0	0.00	0.08	0.27
Chrysothamnus teretifolius	0	0.00	0.04	0.28
Coleogyne ramosissima	0	0.00	0.82	2.43
Echinocereus Engelmannii	0	0.00	0.06	0.24
Encelia spp.	1	0.005	0.61	1.14
Ephedra spp.	8	0.07	4.76	3.19
Eriogonum fasciculatum	3	0.02	1.31	1.92
Eriogonum inflatum	1	0.005	0.12	0.53
Erioneuron pulchellum	7	0.06	0.57	0.94
Ferocactus acanthodes	6	0.05	0.19	0.64
Galium stellatum	0	0.00	0.02	0.14
Gravia spinosa	2	0.01	0.29	0.61
Gutierrezia microcephala	0	0.00	0.31	0.97
Haplopappus Cooperi	2	0.01	1.10	2.04
Haplopappus linearifolius	0	0.00	0.12	0.44
Hilaria rigida	1	0.005	0.36	1.06
Hymenoclea Salsola	0	0.00	0.12	0.39
Krameria parvifolia	1	0.005	1.06	1.38
Larrea tridentata	8	0.07	3.85	2.95
Lycium Andersonii	2	0.01	1.74	1.98
Machaeranthera tortifolia	3	0.02	0.08	0.27
Menodora spinescens	0	0.00	0.53	1.35
Muhlenbergia Porteri	1	0.005	0.08	0.45
Opuntia acanthocarpa	1	0.005	0.31	0.74
Opuntia basilaris	0	0.00	0.08	0.34
Opuntia ramosissima	2	0.01	0.12	0.33
Porophyllum gracile	0	0.00	0.02	0.14
Prunus spp.	0	0.00	0.10	0.59
Psilotrophe Cooperi	0	0.00	0.02	0.14
Psorothamnus Fremontii	2	0.01	0.55	0.89
Salazaria mexicana	1	0.005	0.74	1.04
Salvia Dorrii	0	0.00	0.17	0.80
Salvia mohavensis	0	0.00	0.02	0.14

Table 8 (continued).

Species	Total Freq.	Rel. Freq.	Rel. Cover	SD Cover
Sphaeralcea ambigua	3	0.02	0.10	0.37
Stephanomeria spp.	0	0.00	0.06	0.24
Stipa speciosa	13	0.12	1.74	2.47
Thamnosma montana	1	0.005	0.44	0.98
Viguiera deltoidea	0	0.00	0.17	0.47
Yucca baccata	0	0.00	0.14	0.87
Yucca brevifolia	2	0.01	0.42	0.70
Yucca schidigera	14	0.13	2.31	2.03

Table 9. Frequency and cover of plants in Creosote Bush Scrub, San Bernardino Co., California.

Species	Total Freq.	Rel. Freq.	Rel. Cover	SD Cover
Annual Vegetation	10	0.12	1.38	2.25
Acamptopappus sphaerocephalus	0	0.00	0.07	0.25
Ambrosia dumosa	35	0.38	4.78	3.65
Amphipappus Fremontii	1	0.01	0.08	0.33
Atriplex hymenelytra	1	0.01	0.17	0.74
Atriplex sp.	0	0.00	0.08	0.38
Bebbia juncea	0	0.00	0.05	0.28
Brickellia spp.	0	0.00	0.05	0.21
Cassia armata	0	0.00	0.42	1.12
Coleogyne ramossisima	0	0.00	0.03	0.25
Dyssodia Cooperi	2	0.02	0.03	0.18
Encelia spp.	4	0.04	0.62	1.36
Ephedra spp.	2	0.02	1.07	1.90
Eriogonum fasciculatum	1	0.01	0.60	1.69
Eriogonum inflatum	2	0.02	0.10	0.39
Erioneuron pulchellum	2	0.02	0.18	0.59
Ferocactus acanthodes	2	0.02	0.07	0.25
Gravia spinosa	0	0.00	0.03	0.18
Guitierrezia microcephala	0	0.00	0.03	0.25
Haplopappus Cooperi	0	0.00	0.13	0.59
Hilaria rigida	0	0.00	0.12	0.49
Hymenoclea Salsola	2	0.02	0.48	1.06
Krameria parvifolia	1	0.01	0.88	1.18
Larrea tridentata	10	0.12	6.33	4.35
Lepidium Fremontii	0	0.00	0.02	0.12
Lycium Andersonii	3	0.03	0.90	1.74
Machaeranthera tortifolia	0	0.00	0.03	0.18
Mirabilis Bigelovii	1	0.01	0.03	0.18
Muhlenbergia Porteri	0	0.00	0.07	0.31
Opuntia acanthocarpa	0	0.00	0.22	0.71
Opuntia basilaris	2	0.02	0.08	0.38
Opuntia echinocarpa	1	0.01	0.02	0.12
Opuntia ramosissima	0	0.00	0.22	0.69
Opuntia sp.	0	0.00	0.02	0.12
Porophyllum gracile	0	0.00	0.02	0.12
Psorothamnus Fremontii	0	0.00	0.25	0.50
Salazaria mexicana	1	0.01	0.25	0.67
Salvia Dorrii	0	0.00	0.03	0.25
Stephanomeria spp.	0	0.00	0.03	0.18
Stipa speciosa	0	0.00	0.05	0.28
Tetradymia stenolepis	0	0.00	0.02	0.12
Thamnosma montana	1	0.01	0.03	0.18
Viguiera deltoidea	0	0.00	0.18	0.70
Yucca brevifolia	0	0.00	0.05	0.21
Yucca schidigera	8	0.10	0.78	1.31

Table 10. Frequency and cover of plants in the Dune vegetation type, San Bernardino Co., California.

Species	Total Freq.	Rel. Freq.	Rel. Cover	SD Cover
Annual Vegetation	1	0.03	2.47	5.47
Ambrosia dumosa	0	0.00	0.59	1.36
Croton sp.	0	0.00	0.03	0.17
Ephedra spp.	0	0.00	0.18	0.70
Hilaria ridgida	30	0.81	11.44	7.41
Krameria parvifolia	0	0.00	0.06	0.33
Larrea tridentata	0	0.00	0.15	0.59
Machaeranthera leucanthemifolia	0	0.00	0.03	0.17
Opuntia sp.	0	0.00	0.09	0.28
Oryzopsis hymenoides	1	0.03	0.24	0.54
Opuntia basilaris	0	0.00	0.03	0.17
Panicum Urvilleanum	5	0.14	2.15	3.40
Petalonyx Thurberi	0	0.00	0.06	0.23
Sporobolus flexuosus	0	0.00	0.15	0.49
Tiquilia plicata	0	0.00	0.12	0.40

Table 11. Frequency and cover of plants in the Rupicolous Scrub, San Bernardino Co., California.

Species	Total Freq.	Rel. Freq.	Rel. Cover	SD Cover
Annual Vegetation	4	0.17	0.32	0.82
Ambrosia dumosa	6	0.26	4.05	2.68
Amphipappus Fremontii	0	0.00	0.26	0.65
Aristida sp.	2	0.09	0.37	1.01
Atriplex hymenelytra	0	0.00	0.37	0.90
Baccharis brachyphylla	0	0.00	0.05	0.23
Bebbia juncea	0	0.00	0.32	0.82
Brickellia arguta	0	0.00	0.05	0.23
Ceratoides lanata	0	0.00	0.05	0.23
Coleogyne ramosissima	0	0.00	0.26	1.15
Encelia spp.	0	0.00	1.10	2.00
Ephedra spp.	4	0.17	1.00	1.15
Eriogonum fasciculatum	0	0.00	0.26	0.45
Eriogonum inflatum	0	0.00	0.21	0.49
Erioneuron pulchellum	1	0.04	0.32	0.82
Ferocactus acanthodes	0	0.00	0.05	0.23
Galium stellatum	0	0.00	0.32	0.75
Gravia spinosa	0	0.00	0.26	0.73
Gutierrezia microcephala	0	0.00	0.80	1.72
Hilaria rigida	1	0.04	0.26	0.80
Krameria parvifolia	0	0.00	0.32	0.75
Larrea tridentata	1	0.04	3.47	2.78
Lepidium Fremontii	0	0.00	0.05	0.23
Leptodactylon pungens	0	0.00	0.05	0.23
Lycium Andersonii	1	0.04	1.53	2.76
Machaeranthera tortifolia	0	0.00	0.16	0.50
Muhlenbergia Porteri	0	0.00	0.05	0.23
Opuntia basilaris	2	0.09	0.16	0.37
Peucephyllum Schottii	0	0.00	0.05	0.23
Pleurocoronis pluriseta	0	0.00	0.21	0.42
Salvia mohavenisis	0	0.00	0.21	0.54
Sporobolus flexuosus	0	0.00	0.16	0.50
Stephanomeria spp.	1	0.04	0.21	0.54
Stipa speciosa	0	0.00	0.10	0.32

Table 12. Frequency and cover of plants in the Wash vegetation type, San Bernardino Co., California.

Species	Total Freq.	Rel. Freq.	Rel. Cover	SD Cover
Annual Vegetation	0	0.00	1.73	4.11
Ambrosia dumosa	0	0.00	1.07	1.39
Atriplex polycarpa	0	0.00	0.07	0.26
Bebbia juncea	0	0.00	0.93	2.58
Brickellia incana	2	0.40	1.60	2.35
Cassia armata	0	0.00	0.33	0.90
Chyrsothamnus paniculatus	0	0.00	1.40	2.53
Dyssodia Cooperi	0	0.00	0.07	0.26
Encelia spp.	0	0.00	0.73	1.83
Ephedra spp.	0	0.00	0.13	0.52
Hymenoclea Salsola	2	0.40	7.73	5.23
Larrea tridentata	0	0.00	0.07	0.26
Lycium Andersonii	0	0.00	0.07	0.26
Petalonyx Thurberi	0	0.00	0.20	0.56
Prunus fasciculata	0	0.00	0.13	0.52
Psorothamnus Fremontii	0	0.00	0.53	1.19
Salazaria mexicana	1	0.20	0.27	0.70
Tiquilia plicata	0	0.00	0.47	0.99

Table 13. Frequency and cover of plants in the Transition Zone vegetation type, San Bernardino Co., California.

Species	Total Freq.	Rel. Freq.	Rel. Cover	SD Cover
Annual Vegetation	2	0.05	2.04	2.99
Acamptopappus sphaerocephalus	1	0.03	0.50	1.14
Ambrosia dumosa	5	0.13	2.83	3.97
Amphipappus Fremontii	1	0.03	0.29	0.69
Brickellia arguta	0	0.00	0.12	0.61
Cassia armata	0	0.00	0.17	0.64
Ceratoides lanata	1	0.03	0.25	0.44
Chrysothamnus teretifolius	0	0.00	0.04	0.20
Coleogyne ramosissima	2	0.05	0.83	1.40
Echinocereus Engelmannii	0	0.00	0.04	0.20
Encelia spp.	0	0.00	0.38	0.82
Ephedra spp.	4	0.11	5.17	2.79
Eriogonum fasciculatum	1	0.03	1.00	1.28
Eriogonum inflatum	0	0.00	0.12	0.34
Erioneuron pulchellum	0	0.00	0.08	0.41
Ferocactus acanthodes	1	0.03	0.04	0.20
Galium stellatum	0	0.00	0.04	0.20
Gravia spinosa	0	0.00	0.33	0.76
Gutierrezia microcephala	0	0.00	0.08	0.28
Haplopappus Cooperi	1	0.03	0.62	1.50
Hilaria rigida	0	0.00	0.04	0.20
Hymenoclea Salsola	0	0.00	0.42	0.78
Krameria parvifolia	2	0.05	1.38	1.66
Larrea tridentata	4	0.11	6.92	4.04
Lepidium Fremontii	0	0.00	0.08	0.28
Lycium Andersonii	3	0.08	3.62	2.95
Machaeranthera tortifolia	0	0.00	0.21	0.59
Menodora spinescens	0	0.00	0.08	0.28
Muhlenbergia Porteri	0	0.00	0.04	0.20
Opuntia acanthocarpa	0	0.00	0.08	0.41
Opuntia ramosissima	0	0.00	0.04	0.20
Psorothamnus Fremontii	1	0.03	1.12	1.39
Salazaria mexicana	0	0.00	0.62	0.82
Salvia mohavense	0	0.00	0.04	0.20
Sphaeralcea ambigua	0	0.00	0.29	0.62
Stephanomeria spp.	0	0.00	0.08	0.28
Stipa speciosa	4	0.11	1.00	1.44
Thamnosma montana	1	0.03	0.42	0.51
Viguiera deltoidea	0	0.00	0.08	0.41
Yucca brevifolia	0	0.00	0.21	0.66
Yucca schidigera	4	0.11	1.12	0.99

Appendix B. Causes of mountain sheep mortality

Table 14. Causes of mortality for 9 telemetered mountain sheep, San Bernardino Co., California, 1988-1990.

Animal Number	Sex	Age[a]	Date Collared	Date of Death[b]	Cause of Death
159.225	M	4	27 Sep 87	25 Sep 89	mountain lion
159.235	F	1	25 Sep 87	18 Mar 90	undetermined
159.355	M	7	10 Sep 86	4 Aug 89	accident[c]
159.364	M	6	14 Sep 89	24 Dec 89	undetermined
159.3641	M	8	9 Feb 90	25 Nov 90	mountain lion
159.365	M	2	25 Sep 87	27 Apr 89	undetermined
159.380	M	4	17 Feb 89	18 Nov 90	mountain lion
159.385	M	6	26 Sep 87	24 Jan 88	mountain lion
159.435	M	>10	19 Jan 88	28 Nov 88	undetermined

[a] Age, in years, at time animal was collared.

[b] Median date between when last known to be alive and when mortality signal first received.

[c] Fell into a steep-sided tenaja and drowned.